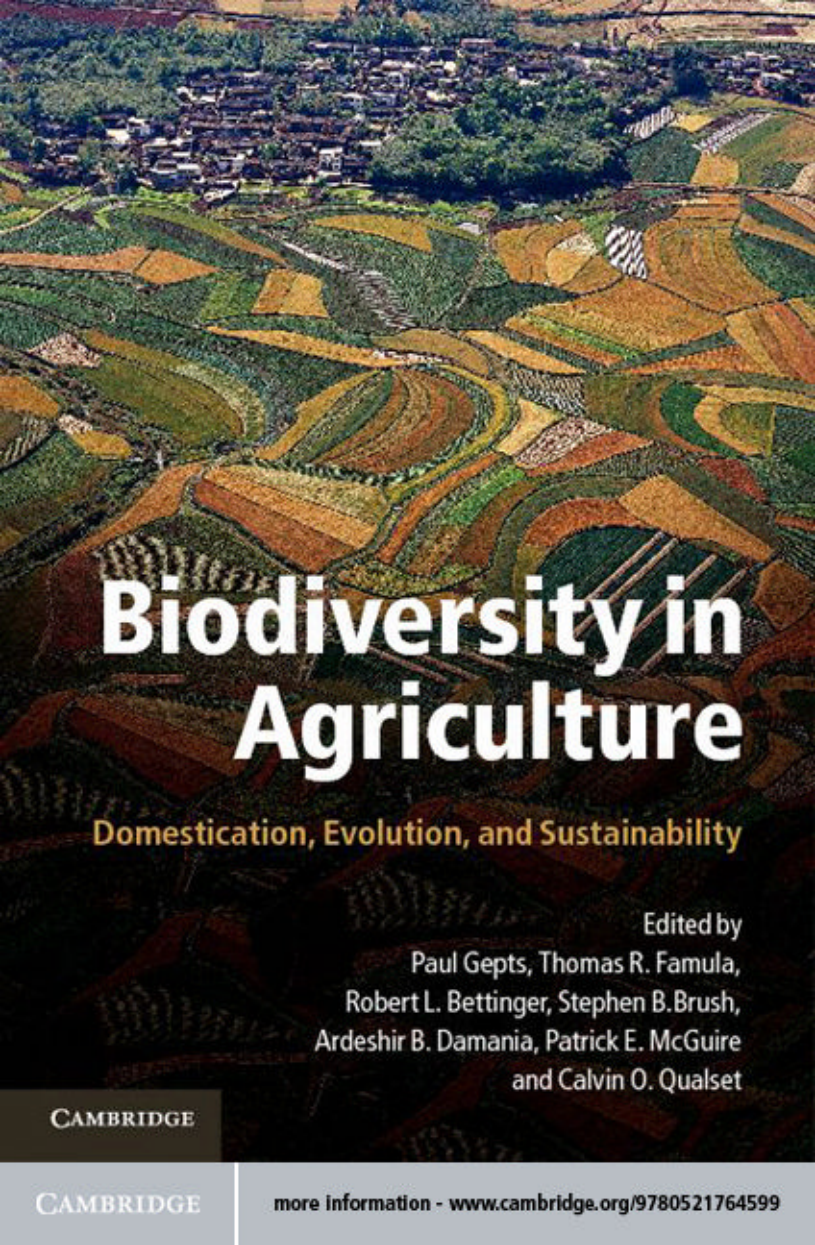


An aerial photograph of a terraced agricultural landscape. The foreground and middle ground are filled with numerous small, irregularly shaped terraced fields in various shades of green, yellow, and brown, indicating different crops or stages of cultivation. In the upper left, a small village with dark-roofed buildings is nestled among trees. The overall scene depicts a traditional, sustainable agricultural system.

Biodiversity in Agriculture

Domestication, Evolution, and Sustainability

Edited by
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Biodiversity in Agriculture

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The introduction of plant and animal agriculture represents one of the most important milestones in human evolution. It contributed to the development of cities, alphabets, new technologies, and – ultimately – to civilizations, but it has also presented a threat to both human health and the environment.

Bringing together research from a range of fields including anthropology, archaeology, ecology, economics, entomology, ethnobiology, genetics, and geography, this book addresses key questions relating to agriculture. Why did agriculture develop, and where did it originate? What are the patterns of domestication for plants and animals? How did agroecosystems originate and spread from their locations of origin? Exploring the cultural aspects of the development of agricultural ecosystems, the book also highlights how these topics can be applied to our understanding of contemporary agriculture, its long-term sustainability, the co-existence of agriculture and the environment, and the development of new crops and varieties.

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Foreword

Bruce D. Smith

This landmark volume eloquently underscores the enduring legacy of Jack Harlan's broad-ranging and multiple-perspective approach to considering the past development and future challenges of agricultural economies, world-wide. It also highlights the remarkable degree to which plant and animal domestication and agricultural origins continue to expand as a general research question across a wide spectrum of different disciplines in the biological and social sciences.

General areas of inquiry are continually emerging in science, and for widely varying periods of time, they attract and reward researchers, providing interesting and unfolding sequences of questions before eventually closing down as their research potential is exhausted. The evolution of agricultural economies, from first origins to future developments, is an excellent example of an extremely long-lived problem area which not only has witnessed substantial growth since the pioneering efforts of Vavilov, Braidwood, Harlan, Heiser, MacNeish, and others, but also holds the very real promise of continuing to expand and provide new research questions for generations to come.

Many of the reasons for this continued expansion of interest and research are obvious. Initial domestication and the subsequent development of agricultural economies was not a single isolated event, for example, but rather occurred in perhaps a dozen different world regions or more, as our distant ancestors independently domesticated a wide variety of different species at different times and in different temporal sequences, providing a rich set of complex regional-scale developmental puzzles for comparative analysis. The subsequent diffusion of domesticates and agricultural economies out of these centers of agricultural origin add to the set of regional-scale comparative examples available for study, with almost every world area experiencing the eventual transition from hunting and gathering to food production economies.

Along with offering complex regional-scale developmental puzzles world-wide, the general research topic of agricultural origins also encompasses the domestication of a rich variety of plants and animals. Each of these in turn provides another complex set of interrelated questions at the species level of analysis for both archaeologists and geneticists: where and when and from which wild progenitor population did different domesticates develop, and in what kinds of environmental and cultural contexts? The past decade in particular has witnessed remarkable advances in our understanding of the early history of a rapidly expanding list of domesticated plants and animals.

Along with establishing clear and lasting templates for how to approach domestication and agricultural origins at both the regional and species levels of analysis, focusing on sub-Saharan Africa and its crop plants, Jack Harlan also framed the central issues involved in the larger-scale comparative analysis of different centers (and noncenters) of domestication. In a series of classic papers, Harlan and colleagues also illuminated the cause and effect of evolutionary relationships at work during the initial domestication of seed plants; how human planting and harvesting of stored seed stock created new sets of selective pressures, with the resultant automatic adaptive response of the cultivated plant populations reflected in the genetic and morphological changes identified today under the general heading of the *adaptive syndrome of domestication*.

Jack Harlan clearly recognized that as a general area of inquiry, *agricultural origins and evolution* encompasses a vast landscape of different research questions and calls for sustained communication and collaboration between researchers in many different disciplines. The Harlan II Symposium, and the rich variety of cross-illuminating perspectives that are represented in this volume, reflect the enduring importance of such scholarly interaction, as well as the continuing expansion of interest in this fascinating and rewarding topic.

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Introduction: The Domestication of Plants and Animals: Ten Unanswered Questions

Paul Gepts, Robert Bettinger, Stephen Brush, Ardeshir Damania,
Thomas Famula, Patrick McGuire, and Calvin Qualset

Some 15,000 to 10,000 years ago, humans started seeding and harvesting plants and maintaining animals in order to augment the food they obtained from wild-growing plants and hunting. These seemingly simple activities set in motion a long-term process that has led to the dominance of agriculture as we know it today. With the exception of a few remaining hunter–gatherer groups, agriculture has now become the most important source of food for most people. Agriculture is also a major source of feed for animals and of fiber.

This transition from hunting–gathering to agriculture was without a doubt one of the most significant eras in the evolution of humans. It allowed food production on a more intensive and efficient scale than ever before, eventually leading to population increases, labor specialization (and especially a nonagricultural sector), the formation of villages, cities, and states, and the rise of more hierarchical societies and states (MacNeish 1991, Barker 2006).

The late Professor J. R. Harlan (1917–1998) understood that the complexity of the biological, societal, and environmental changes involved in the transition to agriculture, as well as their antiquity of up to 10,000 years, necessitated a multidisciplinary approach if one is to understand the factors and processes that have led to the “neolithic revolution.” Anthropologists, archaeologists, climatologists, ethnobiologists, geneticists, geographers, linguists, physiologists, and other practitioners all contribute to the field of crop evolution studies.

J. R. Harlan also expressed concerns that the very development and spread of improved crop varieties were leading to losses in crop biodiversity, well before concerns about biodiversity became common knowledge. He made clear how the knowledge of evolutionary processes in crops facilitated the conservation of biodiversity and its use in the development of improved crop varieties.

The vision of Professor Harlan was the inspiration for the first Harlan Symposium, which took place in 1997 in Aleppo, Syria, at the International Center for Agricultural Research in the Dry Areas (ICARDA). That symposium was remarkable because it brought together plant scientists and archaeologists

(Damania *et al.* 1998). By the way, 1997 is also the year in which the best-selling book *Guns, Germs, and Steel* by J. Diamond, a contributor to this volume, was published.

Since the first Harlan Symposium more than 10 years ago, the communications between archaeologists and both plant and animal biologists have continued, as reflected, for example, in the contributions of Zeder *et al.* (2006a,b). Compared with the first Harlan Symposium, substantial progress has been made in our understanding of crop domestication and evolution, justifying the organization of a second Harlan Symposium. As in other areas of science, such progress has provided answers to existing questions but has also raised new questions.

Among the questions are the following:

1. Why did agriculture originate where it did?

With notable exceptions such as the eastern part of North America (Smith 1995) and Central Asia (e.g., Harris *et al.* 2002), most domestication centers are located in subtropical or tropical regions within 30° latitude of the equator. Diamond (1997) pointed out the rich distribution of wild relatives of crops and farm animals in southwest Asia (the “Fertile Crescent”) and attributed the headstart western European societies had obtained to this distribution. Gepts (2008) has shown that centers of domestication are located disproportionately frequently in biodiversity hotspots (as defined by Myers *et al.* 2000).

Conversely, one can ask the question why other regions with similar geographic and eco-climatic characteristics did not become centers of domestication. For example, although the California Floristic Province supported a rich diversity of Native American cultures, these cultures were only known to manipulate vegetation without actually turning to full-fledged agriculture.

2. What are some of the local ecological or palaeo-ecological conditions, including climate change and human population growth, that would have favored or impeded the transition from hunting–gathering to agriculture?

In addition to the richness in potential crop or farm animal ancestors, other environmental factors could impinge on the agricultural transition. Peake and Fleure (1927) and Harlan (1992, 1995) emphasized the role of biomes with an extended dry season in the domestication of many crops. Storage of harvests could provide a supplement of much-needed food during periods of scarcity, especially towards the end of the dry season and the start of the subsequent rainy season.

However, these general trends do not necessarily speak to the importance of local environmental conditions and their variability in space and time. Flannery (1973) sought to define a role for marginal areas with suboptimal resources (in contrast with nuclear areas) in the origin of agriculture (see also Wright 1992). Suboptimality could result from local population increases as well as a reduction in resources induced by environmental changes (or both).

An additional factor would be short-term climatic events such as the Younger Dryas (11,000 years ago), whose colder and drier conditions may have impelled local, more numerous hunter–gatherers in Southwest Asia and elsewhere to experiment with agriculture (Fuller 2006).

3. Are there specific characteristics in plants and animals that predispose them to domestication?

There are some 400,000 plant species (<http://www.bgci.org/ourwork/1521>, consulted 10 July 2010), but fewer than 500 have been at least partly domesticated (although a larger number is actually used by humans). Are these 500 domesticated species the result of experimentation by early farmers based on some favorable characteristics that stimulated their cultivation?

For example, could only plants that were relatively devoid of toxic compounds have been domesticated? The existence of an extended repertoire of detoxification methods for plant foods (even from wild plants; Johns and Kubo 1988) and numerous toxic crop plants (e.g., cassava, various legumes) suggests that this is not the case.

However, other biological factors may be in play. In many crop species genes for domestication are partly linked. This linkage may have assisted in maintaining the domestication syndrome during the first phase of domestication, marked by cross-pollination (Le Thierry D’Ennequin *et al.* 1999, Gepts 2004).

Or, alternatively, were these species domesticated as a historical contingency, i.e., were they in the “right” place at the “right” time? In the second hypothesis, factors other than ones intrinsic to the domesticate, such as human cultural advancement or the environment, could have played a role. Several of our major staple crops are annual and self-pollinating species. This situation may result from domestication in regions with a marked dry season in which such species may be abundant. In line with this potential historic contingency, some have argued that perennial plants could also be domesticated and become major staples (Glover *et al.* 2010).

Overall, this question remains one of the more tantalizing ones in the field of crop evolution studies. Further experiments are needed to resolve it, especially as the outcome may have important implications for the domestication of new crops.

4. What is the pattern of domestication for crops and animals?

The number and location of domestications of a crop are essential elements to understand not only the origins of agriculture in a particular region of the world, but also the overall distribution of genetic diversity in that crop. For example, a crop may have a single or multiple domestications. The latter may lead to divergent domestication gene pools (e.g., common bean: Gepts *et al.* 1986, Koenig and Gepts 1989, Kwak and Gepts 2009; rice: Sweeney and McCouch 2007). Traditionally, the origin of domestication of a crop has been determined based on the geographic distribution of the wild ancestor, complemented when possible with archaeological remains, which have become much more abundant since the

introduction of the flotation technique (Smith 1995). More recently, the availability of molecular markers (Gepts 1993, Gross and Olsen 2010) has provided an additional tool to identify a more specific area of domestication within the general distribution area of the wild ancestor (e.g., common bean: Gepts 1988, Kwak *et al.* 2009; lima bean (Andean): Gutiérrez Salgado *et al.* 1995; maize: Matsuoka *et al.* 2002; potato: Spooner *et al.* 2005).

There are two caveats, however, in the search for the wild ancestor. First, the analyses are based on the current distribution of the wild ancestor, which may or may not be the same as during the initial phase of domestication. Second, the similarities identified by molecular markers may be due not only to ancestor–descendant relationships, but also to gene flow from the domesticated to the wild gene pool. This type of gene flow is more frequent than generally assumed (Ellstrand *et al.* 1999). Because agriculture represents a production system in which several crops (and farm animals) are assembled, joint information about the origin of the crop and animal components is necessary to fully understand the development of agriculture.

5. What is the timeline of the origins of agriculture? How quickly did agriculture become a major alternative to hunting–gathering?

Domestications in different centers of origin took place roughly some 10,000 years ago. The transition from hunting and gathering to agriculture was clearly not an event, but rather a more-or-less long process. Because the overall inheritance of the domestication syndrome is relatively simple (Gepts 2004), geneticists have proposed that the domestication process could have taken place relatively quickly, i.e., in a time span of several decades to a few centuries (e.g., Hillman and Davies 1999). In contrast, archaeologists and particularly archaeobotanists have proposed a much more gradual transition involving millennia (e.g., Tanno and Willcox 2006). Important factors to address this question would be the actual selection pressure exerted by farmers and the inheritance of the traits involved. This transition included an important phase, predomestication cultivation, a necessary condition for domestication. Determining the actual pace of domestication is an important element in our understanding of the development of agriculture.

6. How did agricultural ecosystems develop?

Most of the focus of genetic studies involves individual crop or animal species. Yet, agriculture is not just the sum of its individual component crops or farm animals. Agriculture is a system consisting of agronomically and nutritionally complementary systems. For example, most centers of domestication include a combination of protein (legume) and starch (cereal or root) staple crops, which provides more balanced nutrition.

Compared with hunting and gathering, agriculture was a more effective way – on a per unit land base – of obtaining food. All other things being equal, one would then expect agricultural societies to take over the world, as indeed they did.

As agriculture expanded, its ecological footprint became larger as well. In turn, this situation has increased the need for a more sustainable type of agriculture that maintains its resource basis.

As agriculture developed, humans became increasingly reliant on it for their food procurement. In turn, agriculture could potentially start exerting selection pressures that affect human phenotypes, such as resistance to malaria, starch consumption, and lactose intolerance (Hancock *et al.* 2010, Holden and Mace 2010). Thus, the agricultural context provides further evidence of continued evolution of the human species (Templeton 2010). Further research is needed, however, to better understand the involvement of humans and the spread of agriculture.

7. How did agricultural ecosystems spread from the centers of origin?

Two, nonmutually exclusive, modes of dispersal have been proposed to account for the spread of agriculture (Ammerman and Cavalli-Sforza 1984, Pinhasi *et al.* 2005). Under the first mode, agriculture was dispersed culturally through adoption by nonmigrating populations of the technology (including the crops). The second mode posits population migration from the center of domestication as the major driver. Although the phenomenon is the best studied in Europe, where the second mode appears to have operated at least for part of the continent (Pinhasi *et al.* 2005), information is also available for the Pacific migrations from east Asia (e.g., McCoy and Graves 2010) but needs to be developed further for other centers of domestication.

8. How can biodiversity be maintained or enhanced in agroecosystems?

Biodiversity is the sum total of biological diversity occurring at various levels of organization, including the infraspecific level, species diversity, the variability of habitats, and the overall variation in the landscape. Replacing native biomes by agricultural vegetation is one of the major factors in the loss of overall biodiversity. When faced with increased demand for agricultural products (whether for food, feed, fiber, or fuel), several responses have been suggested to maintain agrobiodiversity, including creation of biosphere reserves, modifications in agricultural production systems to make them more benign (e.g., shade-grown coffee, hedgerows), and maximizing agricultural production to allow set-aside programs for marginal lands.

Furthermore, agroecosystems can be adapted in such a way that production is increased by applying ecological principles and maximizing the use of agrobiodiversity (Scherr and McNeely 2008, Brussaard *et al.* 2010, Jackson *et al.* 2010). Thus, information about the evolution of crop plants has an important applied component in the development of more sustainable cropping systems. This information will take on added significance in the light of global climate change.

9. How does California benefit from agricultural biodiversity?

The benefits of agrobiodiversity to California are innumerable. As mentioned before, California is not a center of agricultural origins. Yet this state boasts a

very diverse plant and animal agricultural industry. It illustrates the benefits in the introduction of germplasm. Examples are the world-famous wine industry based on judicious choice of varieties adapted to the diverse ecological niches offered by the topography of the state (and the attendant yeast germplasm). Likewise, the dairy industry, based on both animal and forage germplasm, especially alfalfa, has become a major part of the agricultural sector. In addition to alfalfa, many other California crops rely on insect pollinators, whose activity is increasingly threatened.

10. What can crop evolution studies tell us about the potential for future domestications?

Finally, the information gathered in crop evolution studies can help us consider the following situations. How do we expand the repertoire of domesticated species? The current repertoire is limited compared with the total number of plant (and animal) species. It is clear, however, that as human needs increase, there are new opportunities for domestication. These include tree domestication in agroforestry and novel crops for biofuel production. It may also involve re-domestication of existing crops for novel purposes.

The presentations of the second edition of the Harlan Symposium, held September 14–18, 2008, on the campus of the University of California, Davis, that most directly addressed the above questions have been assembled into this volume. The members of the editorial committee would like to thank all the authors for their contributions and patience during the editorial process. We look forward to the next edition of the Harlan Symposia, which will no doubt bring further exciting advances in the field of the origins of agriculture and crop and animal domestications.

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1 The Local Origins of Domestication

Jared Diamond

Plant and animal domestication, which began by about 10,000 years ago, caused the biggest changes in human lifestyle in the past 2 million years. It resulted in the largest and most rapid increase in our population numbers, technology, and political and social complexity in our history. Its consequences were even larger than those of the mastery of fire or the development of writing. In this chapter, I discuss the paradox of why domestication nevertheless arose in only a few areas of the world, and I identify two still unsolved problems about why domestication began in the particular parts of the world where it did. Literature references will be found in the Further Readings section of my book *Guns, Germs, and Steel* (Diamond 2005).

There are three reasons for the big consequences resulting from domestication. First, in a wheat field or sheep pasture, all of the plants and animals are edible to us, but in natural habitats only a few of the plant and animal species are edible, so domestication meant much more edible food per unit area and the capacity to feed many more people per unit area. Hence farmer population densities are typically between 10 and 1,000 times those of hunter-gatherers. Second, domestication meant that people who formerly had to be nomadic to follow seasonal variations in food supply could now settle down in permanent villages next to their fields or pastures, so we became able to accumulate heavy nonportable technology like printing presses and atomic bombs, and (even before that) to shorten our birth intervals and pump out new babies faster. Finally, domestication produced food surpluses that could be stored to feed non-food-producing specialists, such as kings and bureaucrats, metal-workers and potters, and professional soldiers and scribes. For example, one American farmer today produces enough food to feed 125 nonfarmers, and even one Egyptian farmer in the times of the Pharaohs could feed five nonfarmers.

Granted, even before the beginnings of domestication, some hunter-gatherer societies in especially productive and stable environments had already settled down in villages and supported chiefs. Examples include Indians of the Pacific Northwest, the Calusa Indians of Florida, Mesolithic Swiss lake-dwellers, and others. But none of those affluent hunter-gatherer societies advanced as far as

developing kings, metal tools, and writing. Those advantages of superior numbers, armies, technology, and political and military organization let farmers expand at the expense of hunter-gatherers during the past 10,000 years, until by the twentieth century the only hunter-gatherers left in the world were confined to areas unsuitable or marginal for farming.

Given that domestication brings such huge advantages to farmers compared with hunter-gatherers, why didn't domestication arise in all parts of the world? Why didn't some people in every region stumble on domestication and thereby become able to push out or conquer the region's hunter-gatherers? In fact, domestication arose independently in only about nine parts of the world ("homelands of agriculture"): the Fertile Crescent, China, Mexico, the Andes and Amazon, the eastern United States, the New Guinea Highlands, and a few other areas. It is striking that domestication did not arise independently in any of the breadbaskets of the modern world, such as in California, the Great Plains, western Europe, Japan, Java, and the pampas of Argentina. Why not? Was that failure of domestication to arise in all of those modern breadbaskets because of limitations of the local people themselves, or because of limitations of the local wild plant and animal species available to them for domestication?

The latter turns out to be the correct explanation. There were a few areas where local hunter-gatherers became food-producers when nonlocal domesticates arrived from somewhere else. For example, some of southern Africa's San hunter-gatherers acquired cattle and sheep from the north in Africa and thereby became herders, and there may be other cases in western Europe. But, much more often, farming outside of the homelands of domestication appeared when established farmers from the homelands spread out. However, those expanding farmers began farming with crops that they carried from their homeland of agriculture, and not by figuring out how to domesticate locally available wild species outside the homelands. For instance, modern farmers of European ancestry in California are not growing native Californian oak trees and creosote bushes and grizzly bears that they succeeded in domesticating; instead, they grow Fertile Crescent grapes and sheep and other domesticates that they brought into California from the ancient homelands of agriculture elsewhere.

But how can we really be sure that the limitation on the development of agriculture outside its ancient homelands really was the unsuitability of local wild plant and animal species for domestication? There are several lines of evidence.

One line of evidence is that few nonhomeland wild species have been domesticated by arriving experienced farmers from the homelands, despite much effort. For instance, farmers of European ancestry have tried hard to domesticate zebra and eland in Africa, elk and moose in Europe, and bison and musk ox in North America, but with little success: later, I shall say more about the problems encountered in domesticating zebra and bison. Local hunter-gatherers all over the world have known and used virtually all local wild plant and animal species for thousands of years. They even managed to tame African and Asian elephants,

giraffes, rhinos, grizzly bear cubs, hyenas, and cassowaries; and hunter-gatherers everywhere know hundreds of local plant species and their medicinal value and other uses. But all valuable plant and animal species that could be domesticated were domesticated long ago. All of the modern additions to the world's list of domesticates have been of relatively minor value: some small mammals like chinchillas, rabbits, laboratory mice, and hamsters; and some crops like strawberries, cranberries, macadamia nuts, and pecan nuts; but nothing remotely as valuable as the ancient domestication of cows and pigs and sheep, and of wheat and rice and corn.

A second line of evidence for the limitations posed by the wild species locally available for domestication outside of the homelands is the behavior of local farmers when superior domesticates did become available: they often discarded their local crops or relegated them to a minor role. For instance, there was extensive replacement of eastern USA domesticates like sumpweed, domesticated locally 3,500 years ago, when Mexican corn, squash, and beans finally became available in the eastern United States about 1200 years ago and triggered the explosive rise of Mississippian mound-builder societies; and there was widespread adoption of South American sweet potatoes by New Guinea Highland farmers around 500 years ago when sweet potatoes reached New Guinea.

That evidence for limitations posed by local wild plant and animal species available for domestication comes from the behavior of local people. What about evidence from the local wild plant and animal species themselves? What makes some wild species especially suitable for domestication, while most other wild species remain unsuitable? And why were the suitable species concentrated in just approximately nine relatively small homelands, which aren't even leading areas in world agriculture today? Why have we had domesticated almond trees for 6,000 years whereas we still have no domesticated oak trees, despite the important role of wild acorns as staple food in the diets of hunter-gatherers in California, Japan, Europe, and elsewhere? Why have we had domesticated horses for 6,000 years, and cows for 10,000 years, while we still don't have domesticated zebras or bison?

For plants, the most detailed systematic study addressing this question is Mark Blumler's (1992) analysis of cereals, i.e., wild grass species other than bamboos, with edible starchy seeds. There are thousands of such wild grass species around the world. Only a few of them were domesticated, but those few – notably, wheat, barley, rice, and corn – provide about half of all calories consumed by humans today. Around the world, Blumler tabulated the 56 wild cereal species with the largest seeds: i.e., the world's most valuable wild cereals. It turned out that they are mostly native to Mediterranean zones or other seasonally dry environments, which select for grass species with large seeds and an annual life cycle and low investment in inedible wood or stems. Of those 56 large-seeded wild cereals, the astonishingly high number of 32 species is concentrated in western Eurasia's Mediterranean zone, whereas there are only 1 to 5 species each in North America, Meso-America, South America, Australia, and sub-Saharan Africa and their

Mediterranean zones. Three of those 32 large-seeded wild cereal species of the western Eurasian Mediterranean zone – emmer wheat, einkorn wheat, and barley – became among the world’s major crops.

I don’t know of a comparable systematic worldwide study of the number and distribution of valuable potentially domesticable wild species for any other group of plants. Perhaps the next most promising group to analyze in the way that Blumler analyzed wild cereals would be wild pulses, or annual legumes. They are nearly equal to cereals in their human importance, because of their high protein content. Among the many pulse species that were domesticated were peas, lentils, chickpeas, soybeans, American *Phaseolus* beans, faba beans, groundnuts, grams, and others. What we need, modeled on Blumler’s study of wild cereals, is a survey of the world’s wild pulse species with the largest seeds and perhaps other characteristics useful for domestication, such as self-pollination. Again, in wild pulses just as in wild cereals, the Fertile Crescent of western Eurasia was well endowed: its pulses domesticated in the first wave of domestication were peas, lentils, chickpeas, bitter vetch, and grasspeas, and then faba bean, fenugreek, and others in a second wave.

Those findings beg the question: why is the Mediterranean zone of western Eurasia so well endowed with large-seeded wild cereals and pulses? Mediterranean zones in general select for large-seeded annual plants that can survive and germinate after a long hot dry summer, and that don’t invest much in woody or fibrous stems. But why, given this advantage of Mediterranean zones in general, is western Eurasia’s Mediterranean zone so much more rich in large-seeded wild cereals and pulses than the world’s four other Mediterranean zones, in southern California, Chile, South Africa, and southwestern Australia? Why isn’t southern California’s Mediterranean zone famous for its own native species of wheat and peas?

The explanation is geography, as becomes obvious from looking at a world map of habitats or climates. Western Eurasia has by far the world’s largest Mediterranean zone, the one extending by far the farthest inland from the oceans, and the one with the widest range of altitudes and greatest climatic variation within and between years. As a result, the western Eurasian Mediterranean zone is the one with the highest diversity of species, with the highest percentage of annuals, and with the highest percentage of large-seeded annuals to cope with that climatic variation.

For wild animal species, compared with wild plant species, we know perhaps more about the characteristics making them suitable or unsuitable for domestication, but we know less about why species with those characteristics are concentrated in certain parts of the world.

At least seven characteristics contribute to explaining why some wild animal species are potentially more suited to domestication, and yield more valuable domesticates, than do other wild animal species.

1. It helps, as far as we humans are concerned, for an animal to be big. Rabbits and laboratory rats are nice domesticates for some purposes, but they aren’t

useful to pull plows and carts, or to yield milk, or to yield hundreds of pounds of meat. The most valuable domestic mammals are big ones, weighing from 100 to 200 pounds (50–100 kg) for sheep, goat, reindeer, and llama, up to a ton for large cattle.

2. To be domesticated and grown in a barnyard, an animal has to have a diet that we humans can economically supply. Hence we still have no domestic anteaters or giant pandas, because we can't cheaply provide tons of ants and certain bamboo species as fodder.
3. The animal has to grow rapidly: no farmer would want to wait 15 or 20 years for his barnyard gorilla or elephant to become full-sized, feeding and caring for it all those years, before the gorilla or elephant would be ready to send to the slaughterhouse. One may immediately object: what about the African elephants with which Hannibal crossed the Alps, and what about the Asian elephants still used as work and riding animals in Southeast Asia? That brings up the important distinction between just taming (capturing a wild-born animal, and training it to obey humans) and actually domesticating (breeding animals in captivity, and selecting individuals to modify the animal from its wild ancestor so as to make it more useful to us humans). All of Hannibal's war elephants, and all of Asia's work elephants, have been wild-born individuals that have been captured and tamed: why would anyone go to the trouble of feeding a baby elephant and caring for it for 20 years until it is full-sized, when you can save yourself all that work just by capturing wild elephants and taming them?
4. To be domesticable, an animal species must be one that breeds readily in captivity. Some animal species have finicky mating habits and are very difficult to breed in captivity; for example, only within recent decades has it become possible (with great effort) to breed cheetahs and vicuñas. Hence we still don't have domestic cheetahs and vicuñas, despite their great value for hunting and for wool, respectively. Do you think that human hunters and weavers would waste time with lousy racing greyhounds and merino sheep if they could easily breed cheetahs and vicuñas?
5. To be safe to keep in your barnyard, your domestic animal has to be predictably docile. When your animal reaches the right age to be slaughtered, you have to be able to count on your being able to slaughter it, rather than worrying about its slaughtering you first. Hence we still have no domestic grizzly bears, even though they would otherwise be great barnyard meat production animals because they grow quickly and can be fed on garbage. The Ainu people of Japan routinely raised bear cubs to one year of age, and didn't dare to grow them for longer.

We also still don't have domestic zebras, despite efforts to domesticate them for over a century by experienced European stockmen and animal breeders living in Africa. I'm often asked why we don't have domestic zebras. Friends send me photos depicting Lord Rothschild riding through the streets of London in a cart drawn by zebras, and photos of a wagon drawn by a team of eight

zebras in South Africa. Yes, there have been a few cases of zebras being hitched to carts. According to an African friend of mine, a zebra has also carried a child as a rider, though a zebra's back is said not to be strong enough to bear the weight of an adult human. However, when I was on the Animal Management Committee of the Los Angeles Zoo, I was told that the zoo animal that each year kills or cripples the most zoo-keepers in the United States is not tigers or elephants but – zebras. They have the nasty habit of biting humans who come within reach, and not letting go until the person is dead. They defend themselves against lions by a kick with the hind legs that breaks the lion's jaw; such kicks are bad for humans too.

Friends to whom I relate these facts still won't give up hope of domesticated zebras. They object: sure, wild zebras are nasty, but so are wild horses. Americans who keep tamed zebras insist that their reputed nastiness has been exaggerated. If we would just be patient and breed them for a few decades, they would become gentle: that has already happened recently with Arctic foxes, which in just a few decades of selective breeding in Russia in the twentieth century became gentle domesticated fur-bearing foxes. But the fact that you can quickly select one animal species for gentle behavior doesn't mean that you can quickly select any animal species for gentle behavior. Western Eurasian people from ancient Mesopotamians to the Romans gave up on another wild equid species, the onager, after thousands of years of attempts to raise those incurably nasty beasts. The Ainu of Japan didn't succeed in selecting for gentle grizzly bears even after thousands of years of loving care lavished on bear cubs.

6. For a wild animal to be domesticable, it helps for the species' social structure to be based on a herd with a well-defined dominance hierarchy and follow-the-leader behavior among subordinate individuals. Animals with that behavior are prone to accept a human, even a little shepherd child, as the leading alpha individual, and to let a human take over the herd. Hence we have had domesticated Eurasian mouflon sheep for over 10,000 years, but we still have no domestic North American bighorn sheep, which lack that submissive follow-the-leader behavior.
7. Finally, it's bad for your would-be-domesticated wild animal to panic when it sees itself fenced in, and to bash itself to death against the fence. Hence we still lack barnyard gazelles, although they used to be the major prey species of Fertile Crescent hunters.

In light of all those considerations, why don't we have domestic bison? You may immediately protest: but captive bison are ranched extensively in North America, and ranched bison meat is widely available now in American supermarkets. In reality, modern ranched bison are still really fenced animals unmodified or little modified from wild bison, except for some hybridization with cattle. In fact, there are two species of bison, one in North America and the other in Europe, and neither has been domesticated despite all the experience of North American and

European cattlemen in raising cattle which are closely related to bison. What is the difficulty in domesticating bison?

It turns out that there were two problems that disqualified bison in Native American times, and that still make them hard to manage today. I learned those reasons last April when I visited West Texas A and M University in Amarillo, Texas, where the football team calls itself the Buffaloes and keeps a bison as a mascot to parade around the stadium at football games. During my visit, right there in front of the president's house was an adorable big young bison kept in a paddock surrounded by a steel fence 10 feet high, outside of which were eight undergraduate students whose job it was to take care of the beast and to parade it at football games. Those students told me that they loved their bison, but that it presented them with two challenges. First, from a standing position without a running start, it can jump a fence 6 feet high. That's why it's kept inside a 10-foot steel fence. Until the days of modern steel fences, that challenge would have made it difficult to maintain a one-ton animal that can jump or smash your wooden fence, and that is programmed to want to migrate hundreds of miles twice a year. Second, the students told me that their adorable buffalo is stubborn, irritable, and extremely strong. If it wants to do something or to go somewhere, you have to let it do what it wants and just wait until it stops and is ready to follow your suggestion.

The combined result of those seven criteria is that 14 of the world's 4,000 wild mammal species became valuable domesticates, and that Eurasia ended up with a near-monopoly on big domestic mammals. Around the world, there are 14 species of big domestic mammal: cow, sheep, goat, pig, horse, donkey, reindeer, Arabian camel, Bactrian camel, yak, water buffalo, gaur, banteng, and llama. Of those 14, thirteen are Eurasian, and only one, the llama, is South American.

Why is the outcome so lopsided in favor of Eurasia? Part of the reason is simply that Eurasia has the largest number of species of big wild mammal: 72 species of terrestrial herbivore or omnivore weighing over 100 pounds (50 kg), i.e., "valuable candidates for domestication", as compared with 51 in sub-Saharan Africa, and only 24 in the Americas and one in Australia. That's in turn for two reasons: because Eurasia is the biggest continent, and because most of the large wild mammals of the Americas and Australia, but not of Eurasia and Africa, became extinct upon human arrival in the late Pleistocene.

But that's only part of the answer. Eurasia not only has the largest number of large wild mammals, but it also has the largest percentage of them that became domesticated: 13 out of 72 species, or 18% in Eurasia, compared with only 1 out of 24, or only 4% in the Americas, and none out of 51, or 0%, in sub-Saharan Africa (or perhaps 1, if the debate over the site of donkey domestication becomes resolved in favor of sub-Saharan Africa). We think of Africa as being THE continent of big mammals: say "Africa," and we picture herds of antelope and zebra and Cape buffalo stretching from horizon to horizon in East and South Africa. Why did none or only one of those 51 African species become domesticated?

That difference between 18% and 0% is too big to be dismissed as due to chance. It suggests that there is something about Eurasian environments selecting for mammalian characteristics suitable for domestication, and something about African environments selecting against those characteristics. That's a big unanswered question. It's a question of zoology, but it's still one with crucial consequences for human history. If many of those 51 African wild mammals had been domesticated around 9,000 BC, when Eurasians were starting to domesticate sheep and goats – then, by the time of Christ, Bantu shock troops mounted on rhinos and zebras, and fed on barnyard antelope, would have galloped into Europe and swept away the Roman legions with their puny horse cavalry. But it didn't happen that way. Why not?

I can only speculate about some possible explanatory factors. One is that a substantial fraction of sub-Saharan Africa's area is tropical rainforest, where there are few species of large herd mammals, while much of Eurasia is open habitat where one does find large herd mammals. Another factor is that, in the open dry savanna habitats where one finds the herd mammals for which Africa is famous, the antelope species don't have the follow-the-leader social structure of Eurasian sheep and goats and cattle and horses, lending themselves to domestication, but instead have fiercely territorial males in the breeding season, so you can't keep them captive in crowded enclosures. Still another factor is that recent Eurasia may have supported a somewhat smaller suite of large mammalian predators than has Africa, so Eurasian mammalian prey species may have been under less selection for the nasty behavior that disqualified African zebra from domestication. All these suggestions are speculative, but they could be evaluated by experts in mammalian behavior.

In short, domestication poses a paradox. Domestication provided farmers and herders with power compared with neighboring hunter-gatherers, by supporting much denser populations, more potent technology (including more potent weaponry), and politically centralized decision-making. On all continents, one encounters much diversity among peoples in their receptivity to innovation and change. Hence one might have expected that, in every large region of the world, there would have been some people who would have stumbled on domestication, and who would thereby have become able to conquer or drive out or kill their hunter-gatherer neighbors. But that didn't happen: there are only a few areas of independent domestication, apparently only about nine, around the world – whether one calls them centers, cores, or something else. Why? What was special about those nine or so homelands?

Numerous lines of converging evidence indicate that what made the homelands special was not the characteristics of their original human hunter-gatherers, but instead the characteristics of their locally available wild plant and animal species suitable for domestication. The vast majority of wild plant and animal species don't lend themselves to useful domestication, or to any domestication at all. Systematic studies of the worldwide distribution of domesticable wild species have been carried out for wild cereals and for large wild mammals; we need such studies

for other plant and animal groups, of which pulses seem especially promising. As for how the world's valuable potential domesticates came to be concentrated in the nine or so homelands, we have some understanding for cereals and pulses, but explaining Eurasia's high percentage, contrasting with sub-Saharan Africa's lack, of domesticable wild mammals still eludes us. These questions of zoology, botany, and biogeography had huge consequences for the history of the world's peoples.

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Section I

Early Steps in Agricultural Domestication

Robert Bettinger

This part of our volume is about major processes governing the origin and dispersal of agriculture. The contributors are in accord on many issues, in particular that there is no clear break between hunting and gathering and agriculture, the latter arising from practices that develop naturally as hunting and gathering intensifies. David R. Harris ([Chapter 2](#)), who develops this argument most broadly via a global survey of hunter–gatherer plant and animal management and manipulation, concludes that the forager-to-farmer trajectory is essentially one of increasing geographical reliance on fewer species. Much more detailed treatments of hunter–gatherer intensification and its connection to agriculture in specific regions are presented by George Willcox ([Chapter 4](#)), Ofer Bar-Yosef ([Chapter 3](#)), and M. Kat Anderson and Eric Wohlgenuth ([Chapter 8](#)). Particularly striking here is the contrast between the richly documented accounts of plant use and manipulation in aboriginal California and meager archaeological evidence for what must have been equally intensive plant adaptation ultimately leading to agriculture in the Levant. In a nutshell, we know a good deal more about the details of intensive plant use in California, where agriculture did not develop, than in the Levant, where it did. The reason for these different trajectories remains unclear, as does a means for relating one to the other. Dorian Q. Fuller ([Chapter 5](#)) offers a methodological solution to the latter via analysis of a wide range of morphometric responses to human harvesting and manipulation (e.g., changes in seed size or shape) that are expressed well before a species is considered fully domesticated (e.g., nonshattering wheat). Dolores R. Piperno ([Chapter 6](#)) adds phytolith and starch grain size and morphology to the list of characters known to change directly in response to selection. In theory, such morphometric trajectories should index selective pressures connected with plant intensification and permit meaningful comparison between the “proto-agricultural” California and the agricultural Levant. Anderson and Wohlgenuth present some of these data for California. The problem here is that some species are likely more responsive than others. That Anderson and Wohlgenuth can cite only limited evidence for seed

size change in California, for example, may only be telling us that Californian species are less prone to size increase, and thus less attractive as domesticates. Indeed, this might well explain why agriculture developed in the Levant and not California, the Levant having so many more species susceptible to domestication, an idea that Jared Diamond ([Chapter 1](#)) has already pursued on a global scale to explain the differential distribution of agricultural origins. Peter Bellwood's discussion of agricultural expansion ([Chapter 7](#)) is closely related here, the spread of farming clearly hinging on the crops being farmed, just three of which (wheat, rice, and maize) have demonstrated selective superiority by spreading on a global scale. This has resulted in the increasingly wider geographical distribution of increasingly fewer crops, as Harris observes. The papers in this section provide clear evidence both of how far we have come since the last Harlan Symposium in understanding of evolutionary processes driving the origin and spread of agriculture and how far we have yet to go.

2 Evolution of Agroecosystems: Biodiversity, Origins, and Differential Development

David R. Harris

The emergence and establishment of the world's agricultural systems can be seen in retrospect as a very gradual process in which, through the Holocene, humanity became more and more dependent for food on fewer and fewer species of crops and domestic animals – to the extent that now just three cereal crops, rice, wheat, and maize, provide most of the energy humans derive from plant foods. Much of this dramatic reduction in diet breadth occurred in the twentieth century, and it conceals a 12,000-year history of plant and animal domestications, dispersals, adoptions, and exchanges revealed by biological, archaeological, and ethnohistorical evidence. In recent years new genetic, bioarchaeological, and dating techniques have increasingly been used in investigations of the beginnings of agriculture; in particular there has been an upsurge of research on plant and animal domestication (Zeder *et al.* 2006). At the same time much new archaeological evidence has been acquired of early crops and domestic animals in regions previously largely disregarded in the search for agricultural origins, such as parts of South Asia, tropical Africa, eastern North America and lowland South America east of the Andes (e.g., Piperno and Pearsall 1998, Neumann 2003, Fuller 2006, Smith 2006a,b).

It is now clear that the processes by which systems of agricultural production eventually became established in almost all cultivable areas were more varied and complex than previously assumed, and there are still great gaps in our knowledge of the diverse trajectories that led to the emergence, development and worldwide spread of agriculture. One approach to a better understanding of those trajectories is to examine how many so-called hunter–gatherers enhanced their food supplies by intervening in the life cycles of the plants and animals on which they depended.

As early as 1930 the anthropologist Julian Steward drew attention to one such mode of intervention in a paper he provocatively entitled “Irrigation without agriculture”, in which he described how the Paiute people of Owens Valley, east of the Sierra Nevada in California, annually built temporary dams and dug ditches to water and enhance the growth of wild plants that provided staple foods (Steward 1930, and see below). Since then, study of ethnographic and historical

evidence has revealed a wide array of resource-management techniques practiced by “hunter–gatherers” and there is now a large literature on the subject. These practices included burning, tending, planting, sowing, weeding, tillage, irrigation, drainage, taming, herding, and the domestication of some taxa.¹

1 Intermediate subsistence systems

Recognition that such practices were widespread in the recent past exposed the inadequacy of the conventional either/or categorization of hunter–gatherers and agriculturalists (or foragers and farmers) and focused attention on systems of food procurement and production that combined the management of wild and sometimes also domestic plants and/or animals with hunting, fishing and gathering. Such combinations can be designated intermediate subsistence systems.² Their past existence has long been postulated in evolutionary models of human–animal and human–plant interaction, for example by Rindos (1984:152–66) who interposed “specialized” between “initial” and “agricultural” domestication; Harris (1989, 1996) who labeled the intermediate plant- and animal-management categories “wild plant-food production” and “protection”, the latter including taming, protective herding, and free-range management; and Smith (2001) who described societies that occupied this “middle ground” as engaging in “low-level food production”, subdivided according to the presence or absence of domesticated taxa.

Descriptive evolutionary models of plant–animal–human interaction have heuristic value but they only provide conceptual frameworks that then need to be substantiated with firm evidence. In this chapter, ethnohistorical and archaeological evidence of recent and more ancient intermediate subsistence systems is examined to gain a better understanding of how the assemblages of crop plants and domestic animals were formed that became the mainstay of early agroecosystems. Comparative study of such evidence shows that in most environments nonagricultural societies depended on biotically diverse arrays of plants and animals for their food supply, with some species functioning as staples.

One of the well-known and best-documented examples of such nonagricultural broad-spectrum subsistence, with specialization on a few species, comes from the San people of the Kalahari Desert in southern Africa. Historically, they obtained most of their food from a small number of plants, while also gathering diverse vegetable foods from many more. For example, the !Kung San of the Dobe area in the northern Kalahari made use of over 100 species of edible plant, 23 of which contributed about 90% of the vegetable diet by weight, and one species, the very abundant mongongo nut (*Ricinodendron rautanenii*), accounted for at least half the total (Yellen and Lee 1976:38, 40). Similarly, although without such a high dependence on a single species, the Gwi and Gana San, who occupied the more arid Kade area in the central Kalahari, obtained food from over 60 species, 13 of which were major foods (Tanaka 1976:105–8, 117–18). Thus the San made intensive use of a few species, the availability of which was spatially and seasonally

predictable, but they did not systematically manage those plants to enhance their availability, abundance, and productivity.

For intermediate systems in which food resources *were* managed, ethno-historical evidence, chiefly from North America and Australia, shows that such practices focused on a small proportion only of the wild species that contributed to subsistence. Management of these species to ensure their availability and increase yields took place in the context of continued broad-spectrum resource use. This resulted through time in overall reductions in biotic diversity, as the preferred species made greater contributions to food production in response to increased demand variously generated by sedentary life, population growth, environmental changes, and other factors.

2 Food-resource specialization and management

In an earlier paper (Harris 1977a), I suggested that from early in the Holocene the human population depended for most of its staple food supply on five categories of plant and animal foods that became the main targets of specialized management (although other foods, such as stems, leaves, fruits, fungi, insects, shellfish, reptiles, and birds, also contributed to human diets). I proposed that only three of the five categories had functioned as major pathways toward domestication and agriculture: “roots and tubers” (an imprecise collective term for plant underground storage organs), seeds of grasses and forbs (i.e., other herbaceous plants), and social ungulates or “herd animals”. The other two categories – tree nuts, and fish and aquatic mammals – did not lead in that direction, although they too were often procured and processed by specialized techniques and were sometimes managed to increase their availability and productivity. Many species of nut-bearing tree were managed, and some became important constituents of early agroecosystems, but relatively few were domesticated. Likewise, very few species of fish were domesticated, at least before the twentieth century AD when aquaculture (“fish farming”) began to be developed on a large scale (Nash 2000:461–4, Hedgecock, Chapter 26, this volume). Thus it is the first three food-resource categories that are most relevant to understanding the emergence of early agroecosystems. Ethnohistorical and archaeological evidence of the roles in intermediate subsistence systems of all five resource categories is presented in the following sections.

3 Roots and tubers

A great variety of plants with underground storage organs – taproots, root and stem tubers, corms, rhizomes, and bulbs (modified shoots) – have contributed to the food supply ever since humans first began to use digging implements. The importance of these resources increased when people learned how to process fibrous, bitter, and toxic varieties to render them digestible.

Roots and tubers are organs of vegetative reproduction that perennate in seasonal environments and enable the plants to survive dry and cold periods. They are particularly diverse and abundant in tropical seasonal environments but also occur widely in the equatorial and temperate zones (Harris 1969). Their life forms vary from upright, sprawling, and climbing herbs to woody-stemmed shrubs, exemplified respectively by such major root crops as taro (*Colocasia esculenta*), sweet potato (*Ipomoea batatas*), yams (*Dioscorea* spp.), and manioc or cassava (*Manihot esculenta*). They contribute mainly carbohydrate to human diets, only traces of fat, and generally very little protein, although the potato (*Solanum tuberosum*) contains more protein than most other root crops. Some species, particularly manioc and sweet potato, contain substantial quantities of vitamin C. Dependence on roots and tubers as staple foods was most widespread in the past among tropical foragers, but they were also important resources in temperate environments and their role as sources of starch-rich food was often complemented by animal proteins and fats derived from terrestrial and aquatic mammals, reptiles, and fish.

Archaeobotanical evidence of roots and tubers is in general meager, chiefly because their soft tissues decay quickly and their macro-remains seldom survive sufficiently well to be identified morphologically. Charred specimens are occasionally found, and whole organs or fragments of tissue are sometimes preserved in dry or waterlogged contexts. However, recent advances in parenchyma, phytolith, and starch-grain analysis have provided new techniques for identifying micro-remains and they are now being used to probe the prehistory of root and tuber use, mainly in the tropics (Hather 1991, 2000, Denham *et al.* 2003, Harris 2006: S65–S69, Piperno 2006, Torrence and Barton 2006). For example, in central Panama, phytoliths of arrowroot (*Maranta arundinacea*) and leren (*Calathea allouia*), and starch grains of arrowroot, manioc, and yam embedded in grinding stones, have been identified in preceramic deposits in a rockshelter (Aguadulce) dated to between 7,000 and 5,000 years before present (BP) (Piperno and Holst 1998, Piperno *et al.* 2000). In the highlands of Papua New Guinea, banana phytoliths and taro and yam starch grains dated to c. 10,000 BP have been recovered at a site (Kuk Swamp) in the Waghi Valley where a subsistence system has been documented that evolved through several millennia from broad-spectrum foraging to agriculture based on root-crop cultivation (Denham *et al.* 2003, Denham and Barton 2006, Fullagar *et al.* 2006); and in Sarawak, starch grains and parenchyma tissues from tubers of the yam family and aroid rhizomes have been recovered from deposits excavated at Niah Cave, suggesting that such root foods were part of the diet of rain-forest foragers there in the Late Pleistocene and Early Holocene (Barton and Paz 2007:60–7).

There are many ethnohistorical examples, chiefly from Australia and North America, of the intensive use and management of root and tuber plants within nonagricultural broad-spectrum subsistence systems. Australia, the only inhabited continent without prehistoric agriculture, provides extensive evidence of such

practices, which Yen (1989) referred to as forms of “agronomy.” A great variety of wetland and dryland plants with edible tubers, rhizomes, corms, and bulbs provided food in Aboriginal Australia, many of which were staple sources of carbohydrate (Table 2.1a).

Yams were favored staples in both tropical and temperate regions. They were systematically harvested and their reproduction was enhanced by soil disturbance during digging and by both accidental dispersal and deliberate replanting. Such management of wild “round” and “long” yams (*Dioscorea bulbifera* and *D. transversa*) has been widely observed in northern Australia, for example in the Cape York Peninsula (Harris 1977b:433–37), in Arnhem Land (Jones and Meehan 1989:123–25), and in Melville and Bathurst Islands (Goodale 1982). Historical records show that in southern Australia another species of yam (*D. hastifolia*) was intensively harvested and its productivity managed (Hallam 1989). The rhizomes of water lilies (*Nymphaea* spp.), reeds (*Phragmites australis*), bulrushes (*Typha* spp.), and Austral bracken (*Pteridium esculentum*), the tubers of yam daisy (*Microseris scapigera*) and club rush (*Scirpus* spp.), and the corms of spike rush (*Eleocharis dulcis*) were also staple sources of carbohydrate (Gott 1982, Jones and Meehan 1989:122).

The use of roots and tubers as staple foods in Aboriginal Australia probably long pre-dates the ethnohistorical record, but there is as yet insufficient archaeobotanical evidence to document its antiquity at all comprehensively. However, some remains sufficiently well preserved to allow identification have been recovered and dated: for example, uncharred fragments of water lily rhizomes (*Nymphaea violacea*) and of root tubers of water ribbons (*Triglochin procera*) were recovered from two rockshelters (Anbangbang 1 and Djuwarr 1) in Arnhem Land and dated, at Anbangbang 1, to at least 800 BP (Clarke 1989:69–84). Evidently none of the native roots and tubers that provided food was morphogenetically domesticated, but ten genera include species that were domesticated in other continents (Table 2.1a).

In North America, most of the ethnohistorically documented examples of nonagricultural root and tuber management come from western parts of the continent, principally California and the Pacific Northwest, including the Columbia and Canadian Plateaus (Table 2.1b). Anderson (2005:291–305) has described the great diversity of underground plant foods traditionally harvested by Native Americans in California, most of which were managed by various techniques of digging, watering, selective harvesting, replanting, and burning to maintain and increase their productivity. She refers to some 20 geophytic taxa that yielded edible bulbs, corms, rhizomes, tubers, and taproots. For example, increased production of wild onions (*Allium* spp.), blue camass (*Camassia quamash*), brodiaeas (*Brodiaea*, *Dichelostemma*, and *Triteleia* spp.), yampah (*Perideridia* spp.), lomatiums (*Lomatium* spp.), and bitter root (*Lewisia rediviva*) was brought about by digging, which aerated the soil, separated clusters of bulbs, corms, tubers and other propagules, and reduced weed competition, thus stimulating new growth and increasing populations of the desired species. Burning

Table 2.1. Ethnohistorically documented ‘root and tuber’ plants harvested for food in (a) Australia and (b) western North America

The lists include most of the main taxa but are not exhaustive. Symbols: +, inferred staples managed by burning, digging, replanting; *, genera that include species domesticated in other continents.

(a) Australia	(b) Western North America: California and the Pacific Northwest
Araceae	Alismataceae
* <i>Alocasia brisbanensis</i>	+* <i>Sagittaria latifolia</i>
* <i>Colocasia esculenta</i>	Alliaceae
Compositae (Asteraceae)	+* <i>Allium</i> spp.
+ <i>Microseris scapigera</i>	<i>Bloomeria crocea</i>
Convolvulaceae	+ <i>Brodiaea</i> spp.
+* <i>Ipomoea costata</i>	+ <i>Dichelostemma</i> spp.
+ <i>I. gracilis</i>	+ <i>Triteleia</i> spp.
<i>I. polpha</i>	Compositae (Asteraceae)
Cyperaceae	<i>Balsamorhiza sagittata</i>
+* <i>Cyperus</i> spp.	<i>Cirsium edule</i>
+* <i>Eleocharis dulcis</i>	Cyperaceae
+ <i>Scirpus caldwellii</i>	* <i>Cyperus esculentus</i>
+ <i>S. medianus</i>	Dennstaedtiaceae
Dennstaedtiaceae	<i>Pteridium aquilinum</i>
+ <i>Pteridium esculentum</i>	Hydrophyllaceae
Dioscoreaceae	<i>Hydrophyllum capitatum</i>
+* <i>Dioscorea bulbifera</i>	Leguminosae (Fabaceae)
+ <i>D. hastifolia</i>	+* <i>Lupinus nootkatensis</i>
+ <i>D. transversa</i>	<i>Trifolium wormskioldii</i>
Poaceae (Gramineae)	Liliaceae
+ <i>Phragmites australis</i>	+ <i>Camassia quamash</i>
Juncaginaceae	<i>C. leichtlinii</i>
<i>Triglochin procera</i>	<i>Calochortus</i> spp.
Leguminosae (Fabaceae)	<i>Chlorogalum pomeridianum</i>
+* <i>Vigna lanceolata</i>	<i>C. purpureum</i>
Liliaceae	+ <i>Erythronium</i> spp.
<i>Caladenia</i> spp.	+ <i>Fritillaria</i> spp.
<i>Bulbine bulbosa</i>	+ <i>Lilium</i> spp.
<i>Burchardia umbellata</i>	Portulacaceae
<i>Dichopogon strictus</i>	<i>Claytonia lanceolata</i>
Nymphaeaceae	+ <i>Lewisia rediviva</i>
+* <i>Nymphaea violacea</i>	Rosaceae
Orchidaceae	<i>Potentilla anserina</i>
+ <i>Gastrodia sesamoides</i>	Typhaceae
<i>Pterostylis nutans</i>	<i>Typha</i> spp.
Portulacaceae	Umbelliferae (Apiaceae)
<i>Portulaca napiformis</i>	<i>Conioselinum pacificum</i>
Taccaceae	+ <i>Lomatium</i> spp.
+* <i>Tacca leontopetaloides</i>	+ <i>Perideridia</i> spp.
Typhaceae	+ <i>Sanicula</i> spp.
+* <i>Typha domingensis</i>	<i>Sium suave</i>
+ <i>T. orientalis</i>	

Sources: Anderson 2005, Clarke 2007, Gott 1982, Harlan 1992, Harris 1977b, Irvine 1957, Jones and Meehan 1989, Lepofsky and Lertzman 2008, Peacock 2002, Turner and Peacock 2005, Yen 1989.

harvested patches also helped to eliminate competing grasses and shrubs, recycle plant nutrients, and activate new vegetative reproduction.

Several of the Californian root and tuber plants, such as wild onions, lilies, lomatiums, yampahs, camas, and bitter root, also grow in the forest, grassland, and wetland environments of the Pacific Northwest where species of at least 28 genera provided root and tuber foods. Many species were managed by a variety of plant-manipulation practices (Turner and Peacock 2005, Lepofsky and Lertzman 2008), and they provided staple supplies of carbohydrate (and some protein) that complemented fat and protein obtained particularly from the salmon harvest (Hunn 1982:25–9). As in Australia, none of the indigenous root and tuber food plants in western North America appears to have been morphogenetically domesticated, and fewer of the American genera contain species domesticated as food crops elsewhere (Table 2.1b).

Although it is probable, and often assumed, that roots and tubers have long been staple foods in western North America, archaeobotanical evidence with which to test this assumption has only recently begun to be obtained. For example, in a comprehensive study of Native American plant-food use in central California, Wohlgemuth (2004a) recovered charred brodiaea corms from a series of archaeological sites around San Francisco Bay and in the Sacramento Valley that date back to *c.* 5500 BP. In the Pacific Northwest there is archaeological evidence (in the Willamette Valley, western Oregon) that roots and tubers were part of the diet by 11,000 BP in the late Pleistocene/early Holocene. There, and at other localities farther north, the intensity of harvesting and processing root and tuber resources fluctuated through subsequent millennia, and by *c.* 2500 BP they were being exploited throughout the region as far north as British Columbia (Peacock 2002, Ames 2005:93–5).

Despite the tendency of roots and tubers to decay more quickly than grass and forb seeds, and the present lack of archaeobotanical evidence of their past use in many temperate and tropical areas, it is clear that they comprise one of the two major categories of plant food in pre-agricultural subsistence systems, and, like grass and forb seeds, they were widely domesticated and many became staple crops in early agroecosystems.

4 Seeds of grasses and forbs

Seeds of herbaceous plants, especially those of grasses and herbaceous legumes or “pulses” (as well as those of many shrubs) have been a major source of human food since techniques were first developed for harvesting and processing them. The plants occur wild in almost all terrestrial ecosystems; they are particularly abundant in seasonally dry tropical and temperate environments, and they include annual, biennial and perennial taxa. Although the seeds (and fruits) of shrubs have been widely gathered as a wild and sometimes staple resource in many parts of the world, shrubs have not been systematically managed in

nonagricultural contexts as widely as grasses and other herbaceous plants (forbs). Grasses and forbs often occur in relatively pure stands, particularly where the growth of shrubs and trees is restricted by soils that are too dry or shallow to favor deeply rooting plants. They also tend to regenerate more quickly after fire than shrubs and trees and to spread at the latter's expense. These characteristics have facilitated the gathering of the seeds of wild grasses and many forbs and they have offered human populations spatially concentrated, easily harvested, and readily stored supplies of food of high nutritional value. The seeds typically provide carbohydrate, protein, and oil in varying proportions, and also vitamins, minerals and fiber. Most cereal grains contain 70%–80% carbohydrate, 10%–15% protein, and very little (<4%) fat, whereas most peas, beans, and other pulses contain less carbohydrate (40%–55%), more protein (20%–25%), and even less fat (<2.5%). When combined, cereals and pulses complement each other because cereals, although quite rich in protein, contain little of the essential amino acid lysine, which pulse protein contains in larger amounts. They provide better balanced nutrition than protein-poor roots and tubers, and combinations of them characterize many pre-agricultural and early agricultural subsistence systems.

In contrast to roots and tubers, the remains of grass and forb seeds are often preserved in archaeological contexts because their harder tissues are less prone to decay and survive more frequently, particularly when they have been charred. They are routinely recovered from archaeological deposits by the flotation method and, if preservation is good, can sometimes be identified to species level. Archaeobotanical research has tended to focus on cereal crops, but more attention is now being paid to the remains of other wild and weedy grasses and forbs, especially since the phenomenon of pre-domestication cultivation was recognized. Evidence that seeds of wild barley, emmer wheat, and small-seeded grasses (as well as acorns) were being harvested and ground 23,000 years ago has been found at the Ohalo II site in Israel (Piperno *et al.* 2004, Weiss *et al.* 2008); and elsewhere in the Southwest Asian Fertile Crescent research has documented the gradual emergence and establishment of seed-crop agriculture through the Early Holocene from *c.* 12,000 years ago (de Moulins 1997, Colledge 1998, Hillman 2000, Nesbitt 2002, Willcox 2004, Savard *et al.* 2006). For example, in the northern Levant remains of morphologically wild cereals, pulses and other edible seeds found at sites dated to between *c.* 10,000 and *c.* 9,000 BP demonstrate that the seeds were systematically harvested and stored. That they were also cultivated near some of the sites can be inferred from the presence of weeds of cultivation, and of wild einkorn wheat, rye, and lentils outside their natural habitats; and a gradual decrease of small-seeded plants such as species of *Polygonum* and *Rumex* suggests that gathering slowly gave way to cultivation of the larger-seeded cereals barley and wheat (Willcox *et al.* 2008). The evidence as a whole indicates that there was a very long period of grass- and forb-seed management during which broad-spectrum gathering and pre-domestication cultivation of some species co-existed, leading to the

(morphologically attested) domestication and eventual preponderance in the Neolithic period of the founder cereal and pulse crops of Southwest Asian agriculture.

Less is known about the antiquity of grass- and forb-seed use in other regions of the world, but there is abundant ethnohistorical evidence that wild stands were widely harvested, particularly in arid and semi-arid parts of northern Africa, Australia and western North America. In summarizing such evidence for northern Africa, Harlan (1989a) reported that over 60 species of grass were harvested by pastoralists and agriculturalists in the Sahara and the Sahel zone (between the Sahara and the northern margins of the equatorial rainforest). Although most of them were gathered in times of scarcity or famine, several were staples that provided large quantities of nutritious and readily stored food: *Aristida pungens* in the northern Sahara; *Panicum turgidum* in the central Sahara; *Cenchrus biflorus* in the Sahel; *Oryza barthii* in swamplands in a latitudinal zone stretching from the West African coast almost to the Nile; *Paspalum scrobiculatum*, a companion weed of domestic rice, in the West African forest zone; and a complex of grasses, referred to as *kreb* or *kasha*, that included *Panicum laetum* and several species of *Brachiaria*, *Dactyloctenium*, and *Eragrostis* in the eastern half of the savanna zone, where Harlan also referred (1989a: 88) to the harvesting of “massive stands of... wild sorghum (*Sorghum bicolor*) [that] must have been much more common in the past”. Various harvesting techniques were used, but none prevented seed dispersal and regeneration of wild stands, and Harlan did not cite any evidence of the deliberate sowing of grasses or of any other forms of wild-grass management. Although most of the detailed data relates to the recent past, there is some archaeobotanical evidence of wild grass-seed use in the region. For example, at least eight genera of grasses were harvested in the eastern Sahara between c.8,000 and c. 6,200 BP (Barakat and Fahmy 1999); a varied assemblage of grass and forb seeds, particularly *Sorghum*, *Echinochloa*, and *Panicum* spp., has been found at the site of Nabta Playa and dated to c. 8,000 BP (Wasylikowa *et al.* 1997); and at the late Stone Age–Iron Age site of Kursakata in northeastern Nigeria large numbers of *Brachiaria*, *Digitaria*, *Echinochloa*, and *Oryza* grains have been recovered from deposits dated to 3,000–2,800 BP (Klee *et al.* 2000).

It has long been known that several cereals and pulses were domesticated in the Sahel zone, principally sorghum, pearl and finger millet, African rice, cowpea, and two species of groundnut (Harris 1976, Portères 1976, Harlan 1989b), but until recently there was very little evidence of when and where in that vast zone these crops were first cultivated. However, research in West Africa is now providing some direct archaeobotanical evidence, in the form of charred remains and grain imprints in pottery. For example, remains of domesticated pearl millet have been identified and dated to c. 4,000 BP in northeastern Mali (Manning *et al.* 2011) and to c. 3,800 BP in southern Mauritania (Amblard and Pernès 1989, Fuller *et al.* 2007), Ghana (D’Andrea *et al.* 2001) and northeastern Nigeria and northern Burkina Faso (Kahlberger and Neumann 2007); and domesticated cowpea has

been found at sites of the Kintampo tradition in central Ghana and dated to c. 3,400 BP (D'Andrea *et al.* 2007). These two domesticates occur in small quantities in assemblages that otherwise contain abundant remains of wild food plants. Between 4,000 and 3,000 BP they probably remained minor components in intermediate subsistence systems that developed, between 3,000 and 2,000 BP, into an agroecosystem that eventually incorporated the full suite of West African cereal and pulse crops.

In the other two regions where grass and forb seeds were extensively harvested in the recent past, Australia and western North America, there is no definite archaeobotanical evidence of any species being domesticated, but there are reports that wild stands were managed by such techniques as burning, sowing, and irrigation. In Australia the seeds of herbaceous plants, principally grasses, were a major source of food for many Aboriginal groups in the arid and semi-arid interior (Allen 1974, Tindale 1977, O'Connell *et al.* 1983, Harris 1984, Cane 1989). Seeds were harvested from some 12 genera of grasses and at least 14 genera of forbs (Table 2.2a).

The ethnographic and historical accounts seldom allow species to be identified accurately, but it is clear that several were staple foods. Nineteenth century travelers' accounts of grass-seed harvesting describe extensive "fields" of *Panicum* and other grasses, and forbs, and the methods used to gather, process, and store them. The seeds were harvested by hand-stripping or by uprooting whole plants before the seeds were fully ripe, and they were threshed by trampling and winnowed by shaking and rocking in wooden or bark dishes. Surplus seeds were commonly stored in skin bags or wooden containers, sometimes in large quantities. Allen (1974:314) mentions c. 1,000 kilograms of grain stored in 17 wooden dishes, and 54 liters of purslane (*Portulaca* sp.) seed in a mud-covered grass bundle. In tropical northern Australia, where roots and tubers, and tree nuts, rather than grass- and forb-seeds, were the main sources of plant food, wild rice (*Oryza meridionalis*) growing in wetlands was harvested on a small scale, for example in Arnhem Land (Jones and Meehan 1989:127–8).

It is difficult to infer from the historical descriptions which genera or species were the principal sources of edible seeds, but judging by the frequency with which they are mentioned it is probable that *Panicum* and *Portulaca* seeds were two of the most widely harvested staples. A much clearer picture of the relative importance of various seed foods in one region – the Great Sandy Desert of northwestern Australia – is provided by a detailed study of traditional seed use undertaken in the 1980s by Cane (1989). The Aboriginal people who formerly lived in the study area obtained food from 70 plant species, 42 of which produced edible seeds, including 15 grasses, three sedges, and 24 other species. Cane assessed the relative dietary contribution of the 42 edible-seeded species and concluded that only nine were of major importance, two of which, the grass *Panicum australiense* and a sedge, *Fimbristylis oxystachya*, were the most important. They often grew together in dense concentrations, produced abundant seeds and regenerated quickly after fire. Nutrient analyses showed that their raw seeds had exceptionally high caloric value and protein content, and they were sometimes cooked together. Within the

Table 2.2. Ethnohistorically documented grasses and forbs harvested for their edible seeds in (a) Australia and (b) western North America

The lists include most of the main taxa but are not exhaustive. Symbols: +, inferred staples managed by burning, sowing, irrigation; *, genera that include species domesticated in other continents.

(a) Australia		(b) Western North America: California and the Pacific Northwest	
Grasses	Forbs	Grasses	Forbs
Poaceae (Gramineae)	Amaranthaceae	Poaceae (Gramineae)	Boraginaceae
* <i>Brachiaria miliiformis</i>	* <i>Amaranthus mitchellii</i>	<i>Agropyron trachycaulum</i>	<i>Amsinckia mensziesii</i>
<i>Dactyloctenium</i> spp.	Chenopodiaceae	+ <i>Bromus</i> spp.	+ <i>Plagiobothrys canescens</i>
+* <i>Digitaria</i> spp.	+* <i>Chenopodium inflatum</i>	<i>Dactyloctenium</i> spp.	+ <i>P. nothofulvus</i>
* <i>Echinochloa colonum</i>	<i>C. rhadinostachyum</i>	+ <i>Deschampsia</i> spp.	Chenopodiaceae
+* <i>Eleusine</i> spp.	+ <i>Tecticornia verrucosa</i>	* <i>Digitaria</i> spp.	+* <i>Chenopodium album</i>
+* <i>Eragrostis eriopoda</i>	Cruciferae (Brassicaceae)	* <i>Echinochloa crus-galli</i>	Compositae (Asteraceae)
<i>E. laniflora</i>	* <i>Lepidium papillosum</i>	* <i>Eleusine</i> spp.	+ <i>C. fremonti</i>
<i>E. tenellula</i>	Cyperaceae	+ <i>Elymus (Leymus)</i> spp.	<i>Blenosperma nanum</i>
* <i>Eriochloa</i> spp.	<i>Cyperus iria</i>	+* <i>Eragrostis</i> spp.	<i>Helianthus</i> spp.
* <i>Oryza meridionalis</i>	+ <i>Fimbristylis oxystachya</i>	<i>Festuca (Vulpia)</i> spp.	<i>Lasthenia glabrata</i>
+* <i>Panicum australiense</i>	<i>Scirpus dissachanthus</i>	<i>Glyceria fluitans</i>	+ <i>Layia platyglossa</i>
<i>P. cymbiforme</i>	Leguminosae (Fabaceae)	+* <i>Hordeum</i> spp.	+ <i>Madia</i> spp.
<i>P. decompositum</i>	* <i>Canavalia obtusifolia</i>	<i>Melica</i> spp.	+ <i>Wyethia</i> spp.
<i>Paspalidium jubiflorum</i>	* <i>Dolichos</i> spp.	+ <i>Oryzopsis hymenoides</i>	Cruciferae (Brassicaceae)
+ <i>Sporobolus actinocladus</i>	* <i>Glycine</i> spp.	<i>O. miliacea</i>	+ <i>Descurainia (Sophia)</i> spp.
<i>S. indicus</i>	<i>Sesbania aculeata</i>	+* <i>Panicum bulbosum</i>	<i>Rorippa</i> spp.
<i>S. lindleyi</i>	Linaceae	+ <i>P. capillare</i>	Labiatae (Lamiaceae)
<i>Triodia basedowii</i>	* <i>Linum marginale</i>	<i>P. obtusum</i>	+ <i>Salvia columbariae</i>
<i>T. longiceps</i>	Polygonaceae	<i>P. sonorum</i>	Loasaceae
<i>T. pungens</i>	<i>Polygonum</i> spp.	<i>P. urvilleanum</i>	+ <i>Mentzelia</i> spp.
	Portulacaceae	+ <i>Phalaris</i> spp.	Onagraceae
	+* <i>Portulaca filifolia</i>	<i>Sporobolus</i> spp.	+ <i>Clarkia</i> spp.
	+ <i>P. oleracea</i>	+ <i>Stipa (Achnatherum)</i>	<i>Epilobium densiflorum</i>
		<i>speciosum</i>	Portulacaceae
			+ <i>Calandrinia ciliata</i>
			Ranunculaceae
			<i>Ranunculus californicus</i>
			Scrophulariaceae
			<i>Castilleja</i> spp.

Sources: Allen 1974, Anderson 2005, Cane 1989, Clarke 2007, Harlan 1992, Harris 1984, Hetzel and Frith 1978, Irvine 1957, O'Connell *et al.* 1983, Tindale 1977.

broad-spectrum subsistence system as a whole these two species appear to have been the principal plant-food staples.

Both in Cane's study and in most of the historical accounts there is evidence that fire was used to clear ground and to promote plant regeneration, but there are almost no references to the use of any other management practices, such as sowing or soil tillage. One exception is Tindale's (1977: 347) report that the Iliaura people of the northern interior dammed natural drainage channels to direct floods more widely over the plains where the best stands of wild grasses grew – a form of rudimentary irrigation that would have sustained and perhaps increased yields.

Attempts to determine the antiquity of grass- and forb-seed harvesting in Australia have focused on the morphology and use-wear of specialized seed-grinding stone implements rather than on analyses of actual plant remains, which are less frequently recovered at archaeological sites. For example, investigations by Smith (1989) and Smith and Ross (2008) of the functions and distributions of seed-grinding implements and of the duration of site occupation in central Australia suggest that use of grass and other seeds as staple foods began about 4,000 BP, and that they were harvested and processed more intensively after c. 1,500 BP, perhaps in response to population growth and expansion of summer-rainfall grasslands; and much earlier seed processing has been inferred from traces of plant tissue and siliceous polish on an assemblage of grinding stones excavated at a site (Cuddie Springs) in southeastern Australia (Fullagar and Field 1997).

In North America most of the detailed ethnohistorical evidence comes from California and the Great Basin where seeds of some 18 genera of grasses and at least 18 genera of forbs were gathered for food by Native Americans (Table 2.2b).

Anderson (2005:256–66) cites many sources that attest to the former importance of seed gathering in California. She describes how the grain was harvested, stored, and processed by beating ripe seeds into baskets, storing them in granaries, baskets, and pits, parching, winnowing, pounding, and grinding them, and sifting the resulting flour before using it to make soups, gruels, and bread. She also comments on how seeds were often saved and later broadcast-sown (in addition to being incidentally scattered during harvesting), and how harvested areas were burned and then sometimes harrowed to encourage seed germination, reduce competition from other plants, and recycle nutrients. These management practices, when repeated many times, favored the growth of grasses and forbs, which responded well to such environmental disturbance, with the result that, over time, biotic diversity was reduced and less diverse, more monospecific patches of vegetation suited to continued seed harvesting were created.

Ethnohistorical evidence from the Great Basin provides further testimony of the former dietary importance of grass and forb seeds. The Shoshoni-speaking tribes studied by Steward in the 1920s and 1930s, particularly the Owens Valley Paiute, depended for their food supply on various combinations of hunting, gathering, and, in some areas, fishing, but throughout most of the region grass and forb seeds

were staples. A wide range of grasses of the genera *Agropyron*, *Echinochloa*, *Elymus*, *Eragrostis*, *Oryzopsis*, and *Stipa*, and forbs of the genera *Chenopodium*, *Descurainia*, *Helianthus*, *Mentzelia*, and *Rorippa* were systematically harvested. The plants were beaten with wooden and basketry paddles to knock the ripe seeds into baskets, and at least some tribal groups increased the productivity of wild stands by sowing, burning, and watering them. Steward (1941:281) reported that seven of the 15 Shoshoni groups he studied sowed grasses and forbs by broadcasting the seeds on alluvial soils following rains or floods. He also described (1933: 247–50) the more elaborate system of irrigation developed by the Owens Valley Paiute, which (as already mentioned) involved the annual construction of temporary dams and ditches that diverted stream flow to enhance the growth of wild food plants. The main purpose of the irrigation appears to have been the production of two root foods, one harvested for its tubers and the other for its corms. Their botanical identification has been disputed, but the two plants, which Steward recorded by their native names, were probably *Cyperus esculentus* and *Dichelostemma pulchellum*. Several grasses and forbs were harvested from the irrigated areas and the overflow zones below them, in particular a species of *Eragrostis* (Lawton *et al.* 1976).

In contrast to the richness of the ethnohistorical record, archaeological evidence of grass- and forb-seed use in western North America is relatively sparse, although it has increased substantially in recent years. Wohlgemuth (2004a) has shown that in interior central California grass seeds, principally canary grass (*Phalaris* sp.), fescue (*Festuca* sp.), hairgrass (*Deschampsia* sp.), and native barley (*Hordeum* sp.), occur frequently at (Middle Archaic) sites dated to between 7,000 and 2,500 BP, and that small-seed use in general became more intensive after 1,000 BP, although it did not do so elsewhere in California west of the Sierra Nevada and Cascade ranges. There is also new archaeobotanical evidence of grass- and forb-seed use east of the Sierra Nevada. The antiquity of the Paiute subsistence system in Owens Valley remained obscure until Bettinger (1977:15) inferred that the irrigation system probably developed after *c.* 1,000 BP, and there is now evidence of grass- and forb-seed use from a site (CA–INY–5276) dated to 3,700–3,200 BP (E. Wohlgemuth, pers. comm. 2008).

Farther east recent excavations at Pie Creek rockshelter in Tule Valley near Elko in the central Great Basin have exposed a sequence that dates back 5,600 years and contains abundant charred seeds preserved in cultural deposits (Wohlgemuth 2004b). Eleven genera have been definitively identified, two of which, goosefoot (*Chenopodium* sp.) and a grass closely resembling wild rye (*cf.* *Elymus* sp.), were present in almost all the flotation samples. The number of genera represented increases through the sequence, and the (*cf.*) rye seeds appear to have been harvested most intensively during the final phase of occupation after 1,450 BP – a change that may reflect the practice of burning followed by sowing recorded by Steward (1938:104) in northern Nevada (Wohlgemuth 2004b:104). The 5,600-year sequence at the Pie Creek rockshelter provides a unique long-term record of grass- and forb-seed use, which, together with other archaeobotanical data from

prehistoric sites in the western Great Basin (e.g., Milliken and Hildebrandt 1997, Reddy 2003), reinforces the ethnohistorical evidence and demonstrates that these foods were important components of human diet in the region throughout the Middle and Late Holocene.

Although California and the Great Basin provide the most comprehensive evidence of systematic grass- and forb-seed harvesting, some species were valued staple foods in other regions of North America even after maize-based agriculture had been introduced. A well-known example is the harvesting of wild “rice” (*Zizania aquatica*) by Native Americans in the Great Lakes region observed by Stickney (1896). He described how the rice was harvested from canoes and the grain dried before being de-hulled and stored in large quantities in bark boxes and skin bags. The antiquity of wild-rice harvesting in the region is not well established, but at excavations of ethnographically identified harvesting sites in northwestern Minnesota charred rice grains were found in hearth deposits and threshing pits associated with sherds of late prehistoric pottery (Johnson 1969); and at the Scovill site in west-central Illinois, dated to *c.* 1,550 BP, fragments of wild-rice grains were found in association with much more abundant remains of hickory and other tree nuts (Munson *et al.* 1971:424).

The systems of wild grass- and forb-seed harvesting described above are examples of intermediate subsistence systems of plant-food procurement and management widely practiced for many millennia, principally in arid and semi-arid environments. They were nutritionally rewarding systems in their own right, not “just” preludes to agriculture, although, like roots and tubers, many species of grasses and forbs *were* domesticated and became founder crops of early agriculture, as did many of the herd animals considered in the next section.

5 Herd animals

Herd animals (social ungulates) have made major contributions to subsistence as hunted prey in systems of wild-food procurement, as managed animals in intermediate subsistence systems, and as domesticated livestock in agropastoral systems of food production. Although many other animals were domesticated for food, as pets, and for other purposes, and some (e.g., chickens, ducks, geese, turkeys, Guinea fowl, rabbits and guinea pigs) became small-scale “household” food producers, only herd animals were domesticated on a large scale and contributed substantially to the differential development of agroecosystems. They did so principally in Eurasia and northern Africa, where goats, sheep, pigs, cattle, asses, horses, reindeer, camel, and water buffalo were domesticated, and on a smaller scale in the Andes in South America, where two camelids, llama and alpaca, were domesticated. Elsewhere in the world wherever herd animals provided food they were hunted and sometimes managed, but not domesticated.

In intermediate systems of animal management, humans modify the predator–prey relationship of hunting in favor of the target species. They do so in two

main ways: by protecting herbivores from carnivorous predators, sometimes by directly reducing the predator populations, for example, by killing wolves that prey on reindeer (caribou) herds; and secondly by improving the herbivores' access to food by burning vegetation to promote fresh growth of herbaceous and woody plants attractive to grazers and browsers. New plant growth after fire tends to contain more protein and minerals than old growth, and herbivores are also attracted to the salty ash left after a burn. Such habitat manipulation by burning favors the herbivore populations over other species, and although it can be regarded merely as a means of improving the human hunters' chances of success, it does constitute a system of loose herd control or "free-range management".

The past extent of free-range management of herd animals in intermediate subsistence systems is difficult to estimate. Most of the potentially relevant ethno-historical evidence relates to the management of semi-domesticated or feral animals by agriculturalists rather than by pastoralists not engaged in, or dependent on, crop production. The clearest example of the latter is the free-range management of reindeer across the tundra and boreal coniferous-forest (taiga) zone of northern Eurasia by such indigenous peoples as the Sami (Lapps) of northern Scandinavia and the Samoyed, Tungus, Yakut, Chukchi, and Koryak of northern Siberia. Ingold (1980) described the varied ways in which these groups combined the keeping of domesticated reindeer with the management of larger free-ranging semi-wild herds. For example, he described (1980:97–9) the practice of the northern Tungus in the taiga zone of keeping – for milk, riding, and pack transport but not for meat – small herds of domestic reindeer that foraged near their owners' settlements and returned voluntarily, attracted particularly by salt provided for them, and he contrasted them with the large herds of semi-wild reindeer managed for meat by the Chukchi and Koryak of the tundra zone, whose herds also included a core of tame animals used for draft purposes. Interbreeding between domestic and semi-wild animals occurred freely in these systems of "carnivorous" and "milch" pastoralism and they were ecologically sustainable ways of providing human subsistence in boreal environments beyond the limits of agriculture. No similar systems developed among the caribou (reindeer) hunters of northern North America, and, as Ingold argued (1980:103–10, 140–1), reindeer pastoralism probably developed in northern Eurasia as a result of the spread through the taiga and on to the tundra of reindeer originally domesticated in the forest–steppe margins of Central Asia in proximity to horse-riding equestrian pastoralists.

Other ethnohistorical examples of free-range management can be cited, but they relate to situations in which the animals, mainly cattle and pigs, are an integral part of agropastoral rather than intermediate subsistence systems. Two examples suffice: management of the mithan (*Bos frontalis*), a domestic, semi-wild Southeast Asian ox that browses and breeds in secondary forests on land formerly cultivated by the swidden farmers who own the animals (Simoons 1968); and of pigs in the Mediterranean islands of Sardinia and Corsica where feral animals live, and are

hunted, and where cross-breeding still occurs regularly between them and domestic pigs kept in villages (Albarella *et al.* 2007).

The antiquity of systems of open-range management – which were precursors of ungulate domestication in the Southwest Asian Fertile Crescent and may have combined with early seed-crop agriculture there – is difficult to determine archaeologically. However, morphometric analyses of early bone assemblages from the region have shown that it is possible to distinguish between “prey” and “harvest” strategies characteristic respectively of hunters and herders. Thus, Zeder’s analysis of goat bones from the highland site of Ganj Dareh in the Zagros Mountains, directly dated to 9,900 BP, has revealed a clear signature of the management of morphologically wild goats (killing of young males and prolonged survival of females) some two millennia before there is evidence, at the foothill site of Ali Kosh south of Ganj Dareh, of morphologically domestic goats (Zeder 1999, 2006). Similar patterns observed in assemblages of sheep bones in the upper Tigris–Euphrates basin likewise suggest that herds of sheep and goats were being managed from *c.* 9,000 BP in the Middle Pre-Pottery Neolithic (PPNB) period (Hongo *et al.* 2005, Peters *et al.* 2005:110–12). Morphologically wild pigs and cattle too were probably managed in parts of the northern Fertile Crescent in the Middle PPNB long before they were domesticated (Rosenberg *et al.* 1998, Hongo *et al.* 2002:154–7, Helmer *et al.* 2005, Peters *et al.* 2005:112–15). The general conclusion to be drawn from these analyses of ungulate bone assemblages is that populations of the founder domestic livestock of Southwest Asian agropastoralism – goats, sheep, pigs and cattle – were managed in semi-wild conditions for very long periods of time before their reproduction was more closely controlled and domesticated breeds established.

In the central Andes there is also evidence that a long period of camelid management preceded their domestication. Zooarchaeological research in the south-central Andes has documented a very gradual process during which a system of protective herding of wild camelids developed that led eventually to the domestication of the llama and the alpaca (Mengoni Goñalons and Yacobaccio 2006). From *c.* 8,400 BP exploitation of camelids intensified and there was a corresponding decrease in the animal-bone assemblages of other taxa. Remains of camelids larger than present-day guanacos have been found at many sites in the region and dated to between 4,400 and 2,000 BP, suggesting that a transition was underway to the herding of domesticated llamas by hunter–gatherers who were becoming more sedentary. In the latter part of the period, between 3,000 and 2,000 BP, more intensive and specialized uses of domestic camelids developed, including the manufacture of textiles from their wool. This recognition in the central Andean zooarchaeological record of a period of pre-domestication camelid management lasting several millennia parallels the trajectory of open-range herd-animal management in Southwest Asia, but in the Andes it did not lead to the integration of the llama and alpaca with crop cultivation in an integrated system of agropastoral production similar to the one that developed in the Southwest Asian Fertile Crescent.

6 Tree nuts

Trees bearing edible nuts occur in most temperate and tropical woodlands and forests. Their harvesting tends to be more predictable, seasonally and spatially, than other less long-lived plants, and the kernels of many species are highly nutritious, containing 20% or more protein, up to 70% oil, and smaller amounts of carbohydrate. Most nuts also store well, although their processing is often laborious, especially if the kernels are bitter or toxic. They have served as staple foods for many hunter-gatherers, particularly in temperate and subtropical ecosystems where nut-bearing species often form more uniform stands than in biotically diverse tropical forests, in which individual trees of the same species tend to be more widely scattered.

The ethnohistorical record from California provides abundant evidence of the intensive use of tree nuts by Native Americans within broad-spectrum subsistence systems. Nuts were harvested from a wide variety of species, particularly oaks, pines, and buckeye (*Aesculus californica*). Nineteen species of oak grow in California (18 *Quercus* spp. and the tan oak *Lithocarpus densiflorus*), of which eight were major sources of edible acorns, and the nuts of many species of pine also provided nutritious food, particularly gray pine (*Pinus sabiniana*), sugar pine (*P. lambertiana*), Colorado pine (*P. edulis*), and the single-leaf pinyon (*P. monophylla*) (Driver 1953, Farris 1993, McCarthy 1993). Stands of oaks and pines were burned with low-intensity fires to reduce undergrowth, promote regeneration, facilitate nut collection, control insect pests, decrease the likelihood of major conflagrations, and encourage the growth between the trees of grasses and other plants with edible seeds. Nuts were harvested by knocking them down before they fell naturally, which had the beneficial results of pruning dead wood, encouraging lateral growth and reducing competition from birds and mammals (Anderson 2005:280–90). Although they were managed in these ways, oaks appear not to have been deliberately planted, probably for two main reasons: first, because of the discrepancy between human life spans and the trees' slow growth, especially the fact that many species take several decades to reach seed-bearing maturity; and second, because the trees are cross-pollinated, resulting in genetic mixing, which reduces the chances of desired features, such as increased seed size or decreased bitterness, being selected and successfully perpetuated by planting (a problem that is circumvented when domesticated fruit trees are reproduced by grafting). Harvesting oaks, pines, and other species seasonally, managing them, and storing the nuts was therefore a more efficient and flexible system of food production than trying to create "domestic" groves by planting their seeds.

Despite the fact that acorns and pine nuts were staple Native American foods, little has been known until recently about the antiquity of their use in California. Now archaeobotanical investigations by Wohlgemuth (2004a) have produced abundant evidence in the form of charred nutshell that acorns, and also nuts

of the gray pine, were being harvested in interior central California east of San Francisco Bay by *c.* 9,800 BP, and in the foothills of the Sierra Nevada by *c.* 9,000 BP. In the former area, *Quercus* is the most ubiquitous taxon in the flotation samples and the evidence suggests that acorn use became intensive from *c.* 4,500 BP onward, with intensive use of grass and forb seeds being added to the “acorn economy” from to *c.* 1,000 BP; and in Owens Valley, where Bettinger (1976) inferred that pine-nut use dated back at least to 1,000 BP, remains of pine nutshell (from site CA–INY–5276) have now been dated to 3,700–3,200 BP (E. Wohlge-muth, pers. comm. 2008).

In the temperate deciduous forests of eastern North America, hickory nuts (*Carya* spp.), acorns (*Quercus* spp.), black walnut and butternut (*Juglans nigra* and *J. cinerea*), chestnuts (*Castanea dentata*), and hazel nuts (*Corylus americana* and *C. cornuta*) were staple foods in prehistoric and early historical times, and their importance is evident from at least 8,000 BP, for example at the Archaic-period Koster site in Illinois (Asch *et al.* 1972, Petruso and Wickens 1984, Talalay *et al.* 1984, Christenson 1986). Large quantities of nut remains have also been recovered from hearths and pits at many later sites, for example at the Middle Woodland-period site of Scovill, also in Illinois, where hickory nuts, walnuts, butternuts, and hazel nuts were the most abundant food remains found in the 92 pits excavated and dated to between 2,000 and 1,900 BP (Munson *et al.* 1971:422). Tree nuts, especially hickories, remained important foods well into the historical period after agriculture based mainly on maize, beans, and squash had spread to most of temperate eastern North America.

Tree nuts, principally acorns (*Quercus* spp.), hazel nuts (*Corylus avellana* and *C. maxima*), and pine nuts (*Pinus* spp.), were also a major food resource in temperate and Mediterranean Europe from *c.* 9,000 BP in the Mesolithic period on into historical times (Lewthwaite 1982, Zvelebil 1994:38–43, and see numerous references in Colledge and Conolly 2007). In Japan, too, archaeological and ethnohistorical evidence shows that tree nuts were major foods in the Jomon period, from at least *c.* 6,000 BP, and were still being harvested, and managed collectively, in mountain villages in the twentieth century AD. Deciduous and evergreen oaks (*Quercus* spp. and *Lithocarpus edulis*), walnut (*Juglans sieboldiana*), chestnut (*Castanea crenata*), and horse chestnut (*Aesculus turbinata*) were the main food species, some of which, particularly horse chestnut, contain high levels of tannic and saponic acids that had to be removed by elaborate processing before the resultant flour or pure starch could be consumed (Takahashi and Hosoya 2002). There is no conclusive evidence that any of the temperate-forest nut trees anciently harvested in North America, Europe, or Japan were domesticated although some have been in more recent times (e.g., hazels and walnuts).

This situation is paralleled by ethnohistorical evidence of intensive use of (undomesticated) tree nuts by some tropical hunter–gatherers. For example, semi-sedentary Australian Aboriginal groups living in the Queensland rainforest used specialized stone tools to process and store toxic and nontoxic nuts of

many species, principally of the genera *Aleurites*, *Athertonia*, *Beilschmiedia*, *Castanospermum*, *Elaeocarpus*, *Endiandra*, and *Macadamia*. The nuts provided staple food for wet-season camps and for annual intergroup ceremonies. Analyses of archaeological finds of nutshells and of starch residues on grinding stones indicate that exploitation of toxic nuts began about 2,600 BP, associated with the beginnings of permanent human settlement in the rainforest, and became more intensive after 2,000 BP (Harris 1987:359–66, Cosgrove 1996, Horsfall 1996, Cosgrove *et al.* 2007).

More generally, it was the fruits of tropical trees, rather than their seeds, that were valued as sources of food by hunter–gatherers (and early agriculturalists), although there are some exceptions such as the oil palm (*Elaeis guineensis*) in prehistoric West Africa and the Brazil nut (*Bertholletia excelsa*) in Amazonia, both of which were incorporated into agroecosystems based mainly on root-crop cultivation (Purseglove 1972:479–82, Shaw 1976:131–2, Piperno and Pearsall 1998:56, 205). Similarly, some temperate-zone Eurasian tree nuts, such as almond (*Amygdalus communis*), walnut (*Juglans regia*), and sweet chestnut (*Castanea sativa*), were gathered in prehistoric times and later domesticated and incorporated into Southwest Asian–Mediterranean systems of agro–pastoralism (Zohary and Hopf 2000:185–90). However, these examples do not negate the general conclusion that specialized systems of aborigiculture, such as orchards and plantations, are a relatively recent phenomenon. Harvesting, processing, and storing tree nuts, rather than planting and domesticating them, was a rewarding intermediate system of food procurement and management well suited to the reproductive system and slow maturation of the trees and to the mobile and sedentary lifestyles of many hunter–gatherers. It is not surprising that it was not, on its own, a pathway to agriculture – although many species of wild and domesticated nut-bearing tree have become important components of agroecosystems.

7 Fish and aquatic mammals

Many different types of aquatic animal contribute to the human food supply. They include crustaceans, mollusks, amphibians, and reptiles as well as fish and mammals, but only fish have contributed staple foods to human diets throughout much of the world ever since techniques were developed to procure them. They are an excellent source of protein and, in many marine species, also fat: in general, freshwater species contain 14%–25% and marine species 9%–26% protein, and some of the latter up to 20% fat. Fish are particularly important in the traditional animal-based diets of people living in high-latitude coastal and Arctic environments where plant foods tend to be scarce. In the temperate zone, and especially in the tropics, fish often complement nutritionally the carbohydrate obtained from roots, tubers, and cereals, especially rice. Aquatic mammals are also valuable sources of protein and fat, and single animals can provide large quantities of food

of high calorific value. They are more restricted in their distribution than fish, and although seals and whales inhabit the tropics as well as mid- and high-latitudes, the other main aquatic species are more geographically restricted: some, such as sea lions and walruses, to temperate-zone and polar seas, and others, such as dugongs (manatees), to tropical seas and rivers, where, for example in tropical South America and the southwest Pacific, the food they provide complements starch-rich root and tuber crops.

Many methods of capturing, processing, and storing fish have been employed by nonagricultural peoples, but, although they often conserve stocks, evidence that they managed fish populations to increase productivity is limited. One example of intervention in fish reproduction is the practice of the Nootka of northwestern North America, who would sometimes transport salmon eggs or smolts to streams where salmon were depleted or absent (Deur and Turner 2005:19), although this appears to have been more a means of conserving a local supply than of increasing production. Australia provides extensive evidence of fish management in the absence of agriculture. In the tropical north, large stone-walled fish traps were constructed at many coastal locations. They trapped fish as the tide fell, thus ensuring and increasing yields. One complex system of traps on Hinchinbrook Island off the northeast Queensland coast covered an area of *c.* 21,600 m², and excavation of a nearby shell midden, which began to be formed *c.* 1,000 BP, yielded remains of mollusks, crabs, and fish including sharks (Campbell 1982). More elaborate pre-European constructions to manage fish, especially migrating eels, at inland locations in southwestern Victoria were described in the nineteenth century and have since been investigated archaeologically. At the site of Toolondo, large artificial channels were traced that extended over three kilometers and connected the separate coastal and inland catchments of two swamps. The channels were designed to regulate seasonal variations in water flow and increase the availability of fish, especially by linking the catchments and extending the range of eel migrations to other swamps and waterways farther inland (Lourandos 1980). This is an impressive example of environmental modification, or niche construction (Smith 2007), to enhance the availability of an important food resource, but it did not go beyond management to direct intervention in the reproduction of the target species and lead to their domestication.

In the past most fisher–foragers would have been familiar with the breeding and migratory behavior of the fish they caught, particularly freshwater and anadromous species. Many species are spatially and seasonally predictable in their behavior, and are relatively easily procured from the land or from boats using nets, hooks, harpoons, traps, weirs, dams, stupeficients, and other methods. Whether fishing is undertaken by seasonally mobile or by sedentary foragers, it is a more immediately effective and rewarding method of obtaining food than confining and managing fish populations in artificial aquatic habitats such as ponds and tanks, so the relative lack of evidence of attempts by fisher–foragers to manage and breed fish in the past accords with expectation.

Most agriculturalists who obtain aquatic foods also procure them in the wild by catching fish, mammals, and sometimes turtles from rivers, lakes, and the sea. But managing fish to ensure a supply and increase production is an integral part of some agroecosystems, for example pond-field cultivation of rice and root crops in tropical southern and eastern Asia and the Pacific. In the Hawaiian Islands, where taro was a staple crop, large stone enclosures or “ponds” in which fish were trapped were constructed at many points on the coast and beside tidal streams. The fish complemented taro in the diet, and taro and other plant products were fed to fish in the ponds (Summers 1964). In ancient China and Mesopotamia fish, mainly carp, were kept in lakes flooded naturally or by irrigation and in ponds constructed for the purpose, and in medieval Europe so-called “stew ponds” were important features of large estates and monasteries. They were dependable sources of protein provided that they were re-stocked regularly with “wild” fish, although some of the ponds were large enough to contain self-replenishing stocks, which could be selected to improve productivity (Nash 2000:456–9). Thus the management of fish in artificial ponds in Europe and Asia did lead to the early domestication of a few species, and fish were also managed in combination with crop cultivation in some traditional agroecosystems, but few species were fully domesticated until very recent times when large-scale aquaculture began to be developed (Hedgecock, Chapter 26, this volume); and aquatic mammals have remained a wild food resource – now greatly reduced by prolonged unrestricted hunting.

8 The differential development of agroecosystems

Until recently it was widely believed that domestication, at least of cereals, had occurred rapidly, perhaps in a few centuries (Hillman and Davies 1990), and this seemed to be confirmed by the apparently sudden appearance of founder crops in the Southwest Asian archaeological record. Now that assumption has been challenged in two ways: by genetic simulations that support a protracted model of crop domestication (Allaby *et al.* 2008), and by archaeobiological evidence of pre-domestication plant cultivation, animal management, and episodic domestication in intermediate subsistence systems that persisted for millennia. At present such evidence is most abundant for the Southwest Asian Fertile Crescent but it is increasing as research progresses in other regions where agriculture developed independently. New research is revealing great geographical and chronological diversity in the emergence of agriculture, and long time intervals between the domestication of individual species, which were only later brought together in ecologically, nutritionally, and culturally integrated agroecosystems. For example, present evidence indicates that the periods between initial domestications and the establishment of agroecosystems based predominantly on domesticates lasted approximately 6,000 years in Mexico and the New Guinea highlands, 4,000 years in eastern North America, and at least 3,000 years in Southwest Asia. It is these

prolonged periods of episodic or sequential domestication, and the gradual construction of productive systems of crop cultivation and animal raising, that functioned as pathways to agriculture. There are as yet few archaeological sequences that clearly demonstrate successive steps along such pathways, and those that do show how variable the trajectories were that led to the emergence and establishment of agricultural economies.

Comparison of the five major food-resource categories that have been the main source of staple human foods sets the scene for examining how different agroecosystems developed, while the ethnohistorical and archaeological evidence of resource specialization and management suggests the context in which initial domestications took place. As has already been emphasized, crop domestication and agriculture arose mainly out of the management of the two major categories of plant-food: roots and tubers, and grass and forb seeds, but this did not occur in all areas where they were staple managed resources. The evidence already reviewed of intermediate subsistence systems in Australia and much of North America shows that they were biotically diverse, finely tuned to seasonal and other local environmental conditions, and sustained over many human generations; and although seed- and root-food plants were managed to increase their abundance and productivity there is no evidence that societies supported by these indigenous systems were, when encountered by Europeans, on the brink of domesticating crops and becoming agriculturalists.

When we examine regions in which transitions from dependence on managed food resources to dependence on domesticated plants and animals did occur, we find regularities in how different agroecosystems produced food supplies from a narrower range of taxa than was available in broad-spectrum and intermediate subsistence systems. Carbohydrate, protein, fat, and other nutrients were supplied in various combinations, in most of which seed and/or root crops were staples, and to which domestic animals and tree crops sometimes contributed. The combinations differed from region to region: cereals, pulses, goats, sheep, pigs, cattle, and tree crops were the main sources of staple food in Southwest Asia, China, and South Asia; cereals, pulses, other forbs, and tree crops in Mesoamerica; cereals, pulses, tree crops, and cattle in the African Sahel zone; roots, pulses, other forbs, and domestic camelids in the central Andean highlands; root and tree crops in New Guinea, the West African forest zone, and lowland northern South America; and forbs in eastern North America (Table 2.3).³

These generalized regional comparisons exclude many other sources of plant and animal food in the diets of early agriculturalists, and they also obscure differences from area to area within each of the ten large regions listed in Table 2.3, but they do draw attention to the variable extent to which the agroecosystems afforded well-balanced diets without continued dependence also on staple foods procured or produced in the wild. Comparison at this level predicts that the systems in which cereals, pulses, and domestic ungulates were integrated ecologically and technologically in the processes of food production, as they were in parts of Southwest Asia, China, South Asia, and Africa south of the Sahara, would

Table 2.3. Main indigenous staple food crops and domestic herd animals of ten major world regions of early agriculture with approximate dates BP of prehistoric introductions of major exogenous domesticates

Major region	Main indigenous staple food crops and domesticated herd animals						Major early exogenous domesticates	
	Roots/ tubers	Cereals	Pulses	Other forbs	Tree crops	Herd animals	Crops	Herd animals
Southwest Asia		Barley Einkorn Emmer Bread wheat	Lentil Pea Chickpea		Olive Fig Date palm	Goat Sheep Pig Cattle		
China		Rice Proso millet Foxtail millet	Soybean			Pig Water buffalo	Barley 4500 BP Wheat 4500 BP	Sheep 4500 BP Goat ?3500 BP
South Asia		Rice Browntop millet Bristly foxtail millet	Mung bean Horsegram Pigeon pea			Zebu cattle Water buffalo	Barley 9000 BP Wheat 9000 BP	Goat 9000 BP Sheep ?4500 BP
New Guinea	Taro Yam			Sugarcane	Banana Pandanus		Sweet potato 300 BP (or 2000?)	Pig 3500 BP
Northern Africa: Sahel zone		Sorghum Pearl millet Finger millet	Cowpea Groundnuts (two species)		Shea butter tree			Goat 4000 BP Sheep 4000 BP
Northern Africa: Forest zone	Guinea yams				Oil palm			
Meso-america		Maize Teosinte	Common bean Lima bean Runner bean Tepary bean	Pepo squash Chili pepper	Avocado			

Table 2.3. (*cont.*)

Major region	Main indigenous staple food crops and domesticated herd animals						Major early exogenous domesticates	
	Roots/ tubers	Cereals	Pulses	Other forbs	Tree crops	Herd animals	Crops	Herd animals
Eastern North America				Marsh elder Goosefoot			Maize 2200 BP Common bean 1000 BP	
Central Andes	Potato Añu Oca Ullucu		Common bean Lima bean	Quinoa Cañihua		Llama Alpaca	Maize 5000 BP	
Northern lowland South America	Manioc Sweet potato Yam Cocoyam Arrowroot Leren			Peanut	Cashew Peach palm		Maize 6000 BP	

Sources: dates in columns 8 and 9 based on information in Ballard *et al.* 2005, Flad *et al.* 2007, Fuller 2006, Li *et al.* 2007, Marshall and Hildebrand 2002, Pearsall 1992, Piperno and Pearsall 1998, Smith 2006a,b.

have the greatest capacity to feed increasing human populations. Also, as I have argued previously (Harris 2003), because they provided nutritionally adequate diets, and were not dependent on regular access to wild staple foods, they were more capable of expanding into new areas than other systems. Furthermore, their inclusion of herd animals and their focus on annually cultivated crops endowed them with a greater capacity to spread than other systems that lacked herd animals, as in Mesoamerica. The systems that were largely based on root-crop cultivation, in association with long-lived tree crops and without herd animals, as in the West African forest zone, New Guinea, and northern lowland South America, had even less capacity to spread into ecologically novel environments. Lacking staple grain crops and regular access to the “mobile” protein and fat that domestic livestock provide, they depended on fishing and hunting to provide the protein and fat needed to complement their carbohydrate-yielding root crops and were thus “anchored” to local wild-animal resources.

At first glance the central Andean system, which included root crops, pulses, two “pseudo-cereals” (both chenopods), and two herd animals (both camelids), appears to resemble the Southwest Asian mixed grain–livestock system, with an inherent capacity to expand, but there is a critical difference. In the Andes the herd animals were not combined with the crops in a fully integrated system of food production. Although the camelids were an important source of meat at higher altitudes, they were more generally valued as pack animals and wool producers, and they were neither milked nor used as draft animals in crop production. This lack of integration, together with the emphasis on root crops cultivated by human tillage with “foot plows”, reduced any tendency for the system to expand, as a whole, into new environments, although some crops did spread individually, such as quinoa and potato into the desert zone along the Pacific coast (Pearsall 1992:196).

The agroecosystem that originated independently in eastern North America differs from the others in the small number and narrow biotic range of its domesticated food plants. Only four seed plants are known to have been locally domesticated although several others, particularly two grasses (*Hordeum pusillum* and *Phalaris caroliniana*) and a forb (*Polygonum erectum*), contributed significantly to the diet (Smith 2006a,b). The four locally domesticated crops were part of a subsistence system in which food production gradually increased as wild-food procurement continued, and it was only after maize reached the region from Mexico by c. 2,200 BP that a more fully agricultural economy developed.

This last example introduces another important variable in the differential development of agroecosystems, namely whether and when species domesticated outside a given region were incorporated into existing systems. Domesticated (and wild) plants and animals have been introduced, for food and other purposes, into pre-existing subsistence systems for many millennia, but particular significance attaches to the arrival of those that have the potential to become staple foods in the recipient systems. Maize is a notable example of a crop that has the capacity greatly to increase agricultural productivity and enhance human nutrition, as it evidently did from about 2,000 BP in much of eastern North America, and as it

also did after it spread southward from its area of origin in southern Mexico from c. 8,000 BP and gradually became a staple crop in much of Central and South America. Other examples of the power of individual domesticates to increase the overall productivity of pre-existing systems of food production include the introduction of pigs and later the sweet potato into New Guinea; of wheat, barley, sheep, and goats into China and South Asia; and of sheep and goats into the African Sahel, where caprine pastoralism was integrated with cattle raising and the cultivation of indigenous cereals and pulses (see [Table 2.3](#) for the approximate dates of these prehistoric introductions).

These examples of prehistoric interregional transfers of crops and livestock are just part of the more general process that led to the establishment of early agroecosystems – the addition of productive plants and animals ecologically, nutritionally, and culturally suited to incorporation into existing systems of food production. This step-by-step process, rather than the creation from the start of unified “packages” of locally domesticated species, was the principal process by which independent agroecosystems were established that were capable of providing adequate food supplies to sustain sedentary and increasing human populations. Those systems that did so most effectively, by combining cereals, pulses, root crops, and livestock in various mixes, and reducing dependence on wild food resources, were the ones that tended to expand, and, in the process, often absorb or eliminate groups of hunter–gatherers. It is not surprising that the system that most effectively integrated the cultivation of cereals and pulses with the raising of herd animals was the one that spread most extensively: the Southwest Asian agropastoral system ([Harris 2002](#)). It spread during the Neolithic period outward from the Fertile Crescent (aided by the latitudinal orientation of the main Eurasian mountain chains) west across Europe, east to Central Asia, and south and east into northern Africa, the Arabian peninsula, and northwestern South Asia. But even this supposed “package” did not spread as a unified whole. Its elements spread differentially as new environmental conditions and varied indigenous populations were encountered. Some crops and livestock proved better adapted to new conditions than others, and novel variants of agropastoralism developed gradually away from the core region in the Fertile Crescent ([Colledge and Conolly 2007](#), [Diamond 1997:180–5](#), [Harris 1998, 2010:225–36](#), [Ammerman and Biagi 2003](#), [Fuller 2006](#), [McCorriston 2006](#), [Zeder 2008](#)).

9

Conclusion

Several broad conclusions can be drawn from this review of some of the ethno-historical and archaeological evidence that illuminates the obscure prehistory of agriculture. First, that the processes of food-resource specialization and management that led eventually to the emergence of agroecosystems originated in intermediate subsistence systems, and that this occurred in ten or more major regions of the world at different times. Second, that only a very small proportion of the

plants and animals that contributed to broad-spectrum subsistence in the Late Pleistocene/Early Holocene were incorporated into early agroecosystems; and that those that became staple domesticated foods represent a narrow selection of taxa from three categories of wild biota: grass and forb seeds, roots and tubers, and herd animals. This relates closely to a third general conclusion: that early agroecosystems were formed slowly as particularly productive domesticates that rewarded investment of human effort with higher returns – some locally domesticated and often others introduced from elsewhere – became major sources of food. This process resulted in many different combinations of crops and livestock, some of which provided adequate nutrition without substantial dependence on wild foods, for example, those that combined cultivation of cereals and pulses with pastoralism, while others lacked that nutritionally optimal combination and were dependent on various combinations of root and tree crops, fish, game animals, and other wild foods.

Such contrasts lead to a fourth conclusion: that early agroecosystems differed greatly in their capacity to support increasing human populations and to expand into new areas. This differential prehistoric spread of agriculture was a complex phenomenon of great significance in the history of humanity (cf. Bellwood, [Chapter 7](#), this volume) and nutritional differences, although they played an important part in the worldwide spread of agriculture, were only one significant factor in that process.

The final conclusion brings us back to the theme of reductions in biotic diversity through the 12,000 years during which humans came to depend for their existence on a progressively narrowing range of foods. The pace of this process varied greatly in space and time, but can be characterized overall as a trend from general dependence on broad-spectrum patterns of hunter–fisher–gatherer subsistence in the Late Pleistocene/Early Holocene, through several millennia in which intermediate systems of resource-management evolved focused increasingly on staple foods, to the emergence and differential development of agroecosystems incorporating mixtures of locally domesticated and introduced crops and livestock. In the course of this gradual evolution of human subsistence, particular plants and animals responded to human intervention in their ecology and reproduction with greater increases in their abundance and productivity than the majority of species being managed, cultivated, and raised: for example, large-seeded cereals, social ungulates that could readily be tamed and were capable of rapid reproduction, and vegetatively reproduced plants with underground storage organs that could easily be selected for increased size and reduced toxicity.

As the food-resource spectrum narrowed and agroecosystems provided more and more of humanity's food supply by occupying a greater and greater proportion of the world's cultivable and grazeable land, it was not only agricultural biodiversity that diminished. As forests were cleared, grasslands plowed, wetlands drained, and deserts irrigated, agricultural expansion brought about a drastic and still continuing reduction in overall biotic diversity. We can now trace, at least in outline, the prehistoric beginnings of this agricultural transformation of the

planet, but as the world's population continues ineluctably to increase and biodiversity to diminish, efforts to develop more diverse and sustainable methods of feeding humanity become ever more necessary.

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Notes

1. In this paper, the term domestication is taken to mean humanly induced morphogenetic and/or behavioral changes that result in increasing dependence of the organism on human intervention in its reproduction. So defined, domestication can potentially be recognized in the archaeological record provided such changes can be identified in animal and plant remains (some of which, such as vegetatively reproduced root and tuber crops, are more difficult to identify than seed-reproduced crops such as cereals). Although this definition is more difficult to apply to some taxa than to others, it also has the merit of drawing attention to the phenomena of pre-domestication cultivation and pre-domestication animal management.
2. My choice of the term “intermediate” (literally in-between) to denote these systems is intended to avoid any implication that they collectively represent a general developmental stage in “progress” toward “agriculture”; indeed, many of them have sustained nonagricultural societies over the long term without domestication. I use the term “subsistence” here to denote systems of procurement and production that have provided humans with their basic supplies of food, while acknowledging the cultural and ecological importance of other food-related behaviors such as social feasting and ritual consumption. My primary aim is to examine and exemplify *how* ecologically and nutritionally effective systems evolved from “hunting and gathering” to “agriculture”, and I have deliberately not addressed here the fundamental question of *why* early agroecosystems developed.
3. The number of regions in which agriculture can be said to have originated independently is matter of spatial scale (as well as of how agriculture is defined (Harris 2007) and evidence assessed). Selection of the ten major regions listed in Table 2.3 is somewhat arbitrary, in that others could plausibly be added in, for example, Africa and South America, and subregions of domestication and early agriculture can be designated within the major ones, for example in China a “millet zone” in the north and a “rice zone” in the south, and in South Asia subregions in the northwest, in the Ganges basin, and in the southern Deccan. But insights into how agriculture originated and developed worldwide can be gained by comparing the major regions that are summarized in Table 2.3.

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3 From Foraging to Farming in Western and Eastern Asia

Ofer Bar-Yosef

The transition from foraging to farming is a process that began during the Late Pleistocene and continued for several millennia during the Holocene in various parts of the Old and New Worlds. From a global evolutionary viewpoint this seems to be just a short time span, but for the individuals who participated in the yearly unfolding of events in their communities, whether they voluntarily adopted farming or were coerced into it, farming probably would not have been an easy adaptation. The advent of farming brought about dramatic socio-economic shifts that we incorporate under the label of the Neolithic Revolution. To understand the great impact of this shift, it is best to compare it to the impact of the Industrial Revolution, just with a slower pace of technological achievement.

The causes of the Neolithic or Agricultural Revolution are highly debated and will not be discussed in detail in this chapter. Suffice it to say that while it was compulsory during the Holocene (Richerson *et al.* 2001), it was already a possible option during the Bølling–Ållerød (*c.* 14,500 to 12,800 BP), a sub-period that punctuated the post-Late Glacial Maximum (LGM) when “demographic pressures” were rapidly building up (Bar-Yosef 1998 and references therein). Thus, the crisis of the cold and dry Younger Dryas (YD) event (12,800 to 11,700/500 BP) forced several territorially coerced populations of hunter–gatherers to initiate a “low level food production” (Smith 2001). The newly initiated or intensified subsistence strategy found its full success during the early millennia of the Holocene.

Over the course of two or three millennia of the Neolithic Revolution, a series of plants were cultivated and, due to genetic mutations, became domesticated. At the same time, other wild plants were grown and consumed. In addition to the vegetal diet, early farmers continued to gather wild plants and fruits, and to hunt and trap locally available game. Only later, after domesticating the first plants, did farmers start to control herd animals, and these, like the founder crops, came to be domesticated.

Hence, the first stage of the Neolithic Revolution at both ends of Asia (Figure 3.1) was characterized by a long period of cultivation of wild plants (e.g., Kislev 1997,

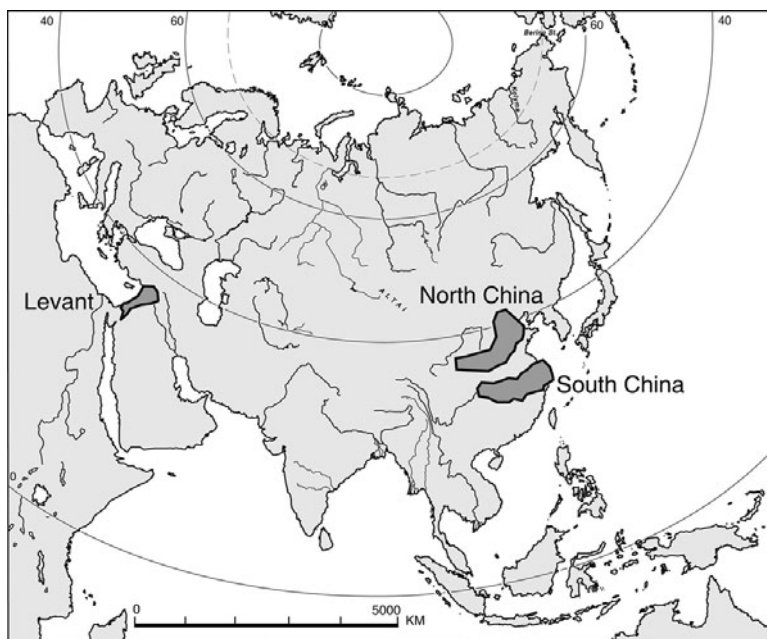


Figure 3.1. The two areas in Asia discussed in this chapter. Note the size differences between east and west.

Willcox 2005, Crawford *et al.* 2006, Bettinger *et al.* 2007, Feldman and Kislev 2007, Harris 2007, Willcox *et al.* 2008, Crawford 2009, Fuller *et al.* 2009) followed by animal domestication. One might expect that after a thousand years or more of cultivation (including sowing, harvesting, and storing seeds), unconscious selection would have been replaced by direct human involvement. The advantages of collecting nonshattering ears of cereals would have driven intentional selection, and the increasing numbers of domesticated plants in fields. The domestication of legumes and flax then followed that of the cereals.

A somewhat similar process in tending herd animals commenced with the almost contemporary corralling of goat, sheep, pig, and cattle in Western Asia that eventually became domesticated (e.g., Vigne *et al.* 1999, Vigne 2008) and pig in East Asia (Yuan and Flad 2002). Dogs were domesticated in both regions during the Terminal Pleistocene. Thus, we should accept that archaeologically the retrieval of arable weeds with the seeds of the main cereal species constitutes the evidence for *cultivation* and thus indicate that prehistoric people were *farmers*, even if it was just a part-time occupation, or as “low level food production” (Smith 2001). The same would hold for the evidence for animal husbandry. None of these changes occurred overnight, as the process of “trial and error” lasted for more than a millennium, and also failed in several cases (Weiss *et al.* 2006). Through the entire time, contact among geographically dispersed human communities continued, and information concerning new ways of treating plants and animals was communicated along routes of several hundred kilometers.

In comparing the courses of observable socio-economic changes in the two Asian regions, we realize that each step in this complex process took a different time span, but the outcome in both regions was a major population growth referred to as the Neolithic Demographic Transition (Bocquet-Appel and Bar-Yosef 2008, and papers therein), with villages increasing in size. The immediate result of this “Neolithic Revolution” was the dispersal of full or partial “agricultural packages” as well as technological ideas to nearby regions and later, to more remote places. One of the better-known patterns of such dispersal is that which occurred across Europe (Colledge and Connolly 2007 and papers therein).

In order to study what happened in the past we employ the various techniques and approaches of archaeology. The collected data can be interpreted by employing scientific techniques such as radiocarbon dating, chemical residue analyses, stable carbon, oxygen and nitrogen isotopes, ancient DNA, and the like. The results from field discoveries are interpreted through inferences from replication studies and ethno-historical observations. Hence, the requirements on current archaeologists in constructing knowledge are no less than the in-depth understanding required of natural scientists and obtained through advanced university degrees and experience. However, sometimes it seems that, owing to the nature of the archaeological study of past societies, interpretations are easy because we intuitively feel that past behaviors replicate our own. Yet there is nothing more misleading than making such one-to-one analogies with the world in which we live today, believing that this is the key to the past. On the contrary, today’s world carries most of its cultural concepts from the past, and thus, the past is the key to the present. We also should not forget that there is immense variability in problem resolving among human societies known from ethno-historic records, and it is the variable solutions that can provide building blocks for models that serve us in understanding the past. Indeed, uncovering the human role of early farmers within their environmental contexts is no less important than understanding the “domestication syndrome” of plants and animals (Brown *et al.* 2008), a process that took many centuries to accomplish.

Disclosing the sequence of socio-economic changes that led particular hunting and gathering groups to start on the path to farming and eventually become fully agricultural societies requires answers to the fundamental questions of “where”, “when”, and “how”. Only when these are answered can we ask the question, “why”. Different answers to the “why Neolithic Revolution?” are already available in the literature of evolutionary biology and anthropology. One example is the debate whether “abrupt climate change” such as the YD triggered, in particular regions, the necessity for major shifts in subsistence strategies. Fortunately nowadays we face the challenges of the projected impacts of “global warming”, and these facilitate a more friendly academic atmosphere to return to the search for how climate, or more specifically, environmental modifications, forced prehistoric foragers to make drastic social decisions in order to minimize risks to their survival (e.g., Bar-Yosef and Belfer-Cohen 1992, Miller-Rosen 2007). In several regions, these social decisions resulted in the emergence of new settlement

patterns, new building techniques, the cultivation of selected plants, the corralling and domesticating of animals, and finally, the acceptance of a new hierarchical social order. In other regions, though, adherence to the old Pleistocene life ways remained a viable option during most of the Holocene. Indeed, although natural calamities can be a cause of changes, the reaction of any social entity to climate change would depend on its history as a society, whether with or without central organization. Leadership, considered essential in historical times, was also essential in facing the challenges encountered in the prehistoric past.

This paper compares the course of human decisions among those who faced the YD and additional Holocene Rapid Climatic Changes (RCC) in West and East Asia. The compared regions are of different geographic dimensions. The area of Southwestern Asia known as the Levant, where the transition to agriculture took place, is approximately 200,000 km². The regions in China are about 500 to 400,000 km² in the north and about 300,000 km² in the south (Figure 3.1). Owing to the rich archaeological experience of the Levant it serves in interpreting the still limited amount of information available from North and South China. It is not surprising that after a century and half of field and laboratory research there are more data sets available in the West than in the East. There is also no need to mention that in a summary such as this, none of the above issues can be dealt with comprehensively. With this in mind, interested readers may find additional information in the list of references.

1 From mobile foragers to the Natufian complex society in the Levant

The archaeology of the late Palaeolithic foragers in the Levant is relatively well known. Prehistoric social units are identified on the basis of detailed lithic analyses combined with other attributes such as site size, site structure, graves and burials, distribution of settlements, and the reconstructed patterns of seasonal mobility. There is a diversity of cultural labels for the entire period until the onset of the Holocene. Several prefer the tri-partite subdivision of the period, known as the Epi-Palaeolithic, into Early, Middle, and Late (Figure 3.2). Others adhere to cultural labels such as Kebaran, Nebekian, Geometric Kebaran, Mushabian, Ramonian, Hamran, etc. The only accepted region-wide cultural designation is the Natufian culture (e.g., Garrod 1957, Bar-Yosef and Belfer-Cohen 1989, Henry 1989, Goring-Morris 1995, Bar-Yosef 1998, 2001, Valla 2000).

In brief, the Late Glacial Maximum (LGM), a cold period that lasted several millennia (*c.* 24,000–18,000 BP), was a major “bottleneck” for the surviving human populations in the Old World. Large portions of Eurasia were deserted. The Levantine conditions were reasonably good when compared to the northern latitudes. The sites of the Kebaran complex (*c.* 19,000 to 16,500 BP), owing to the limiting climatic conditions, were geographically spread only within the coastal Levant, the Taurus foothills, the Euphrates River valley, portions of the Transjordanian plateau, and isolated oases. The spatial distribution of

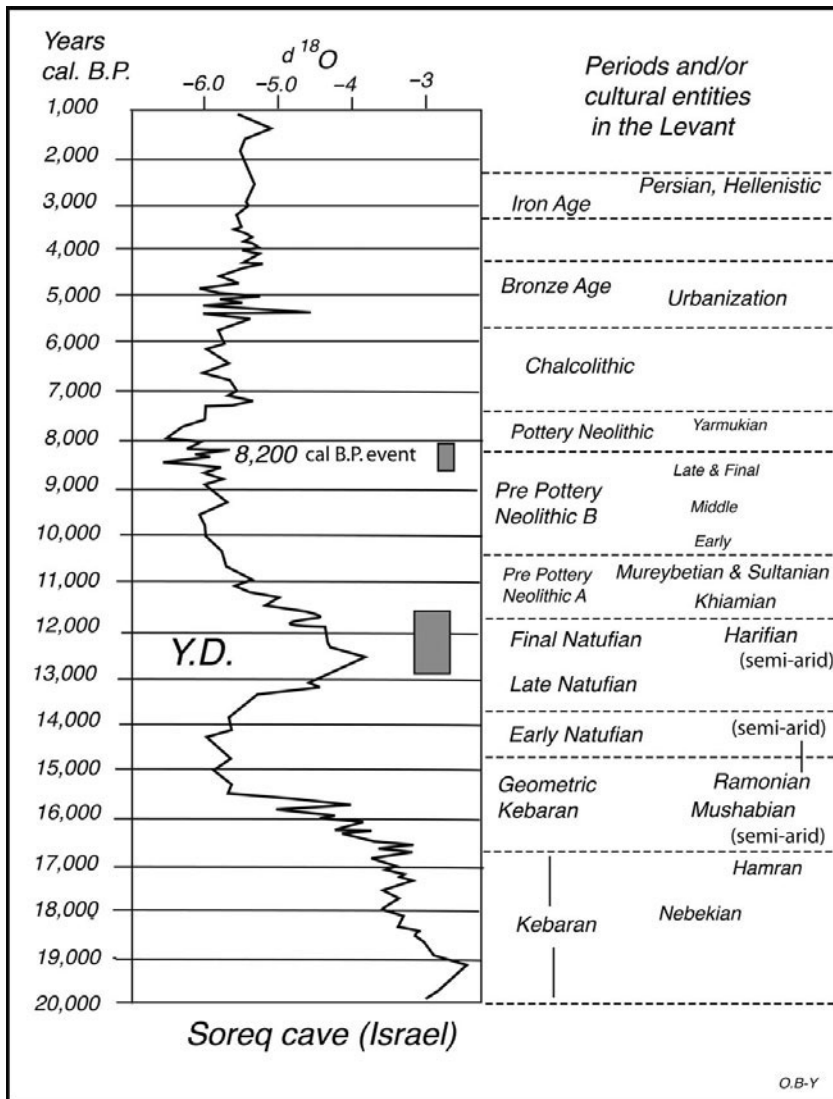


Figure 3.2. Climatic curve from Soreq cave (published with permission of the M. Bar-Matthews and A. Ayalon, Geological Survey of Israel) and the suggested chronological correlations with various prehistoric entities.

sites reflects semi-sedentary occupations of small groups with anticipated seasonal movements.

During the ensuing warming period with increasing amounts of annual rainfall (16,500 to 15/14,500 BP), the Geometric Kebaran foragers took advantage of the climatic amelioration and expanded their dispersal across the entire Levant into formerly desertic environments that became steppic. Other groups of foragers shared with the Geometric Kebarans the vast areas of the marginal belt of the

Syro-Arabian desert in the east. Occupations of a large range of territories, and the encountering of contemporary groups such as the Mushabian and Ramonian hunter-gatherers in Sinai and the Negev (who most probably moved in from NE Africa), may explain what is referred to as a “relative demographic pressure” prior to the emergence of the Natufian culture (Bar-Yosef and Belfer-Cohen 1989, 1992).

Cautious estimates indicate that the exploitation of vegetal resources formed the main dietary intake of Levantine foragers. Charred plant remains were collected in abundance from the waterlogged site of Ohalo II, dated to *c.* 23/21,000 BP, the time of the LGM (Kislev *et al.* 1992, Nadel 2004). The plant assemblage contained a rich suite of seeds and fruits (with a small percentage of cereals). Similar rich assemblages are known from the basal layer (1) of Abu Hureyra (Hillman 2000, Hillman *et al.* 2001), dated to *c.* 12,000 BP and from Mureybet I (Willcox *et al.* 2008). In spite of the time lag between collections they reflect intensified gathering of *r*-selected resources from a variety of habitats and plant associations. Interestingly, Ohalo II inhabitants practiced the same broad spectrum gathering *at least* some 12,000 years before intentional cultivation became a necessity. In addition, food preparation by grinding small seeds mixed with water has been demonstrated with the discovery of starches at Ohalo II (Piperno *et al.* 2004). Groundstone mortars, bowls, cup-holes in limestone slabs, and flat grinding stones were employed in food processing at least since 26,000 BP (in the Upper Paleolithic layers of Qafzeh cave) and became abundant after the Kebaran time (Wright 2000, Belfer-Cohen and Hovers 2005).

Availability of game animals varied by ecological settings, which included Mediterranean forest, woodland parkland, steppe, or semi-arid belts. The most common taxa in the northern Levant were aurochs, onager, deer, wild sheep, and wild goat (e.g., Peters *et al.* 1999), while two species of deer, gazelle, hartebeest, ibex, and hare were frequently hunted in the southern Levant (e.g., Bar-Oz 2004).

The Natufian culture signifies a major threshold in Levantine prehistory. It either emerged as a result of a short-term abrupt cold climatic spell, known in Europe as the Older Dryas, or simply flourished during the improved ecological conditions of the Bølling-Ållerød period, which facilitated the establishment of the semi- and fully sedentary communities that characterize the main Natufian sites. These new agglomerations of humans, with established sense of territorial ownership expressed by intra-site cemeteries, emerged as a reaction to demographic pressures that required a security and defense, whether real or for ritual purposes (e.g., Roscoe 2009). A wealth of archaeological remains of this prehistoric entity, divided into Early, Late, and Final Natufian, has been accumulated since the 1930s (e.g., Henry 1989, Goring-Morris and Belfer-Cohen 1997, Bar-Yosef 1998, 2001, Belfer-Cohen and Bar-Yosef 2000, Valla 2004).

Natufian hamlets are found in their supposed “homeland” area located within the oak-pistachio woodland belt, where the herbaceous undergrowth contained high frequencies of cereals. Late Natufian semi-sedentary occupation was recently uncovered in Dederiyeh cave in the mountains of northern Syria (Nishiaki *et al.* 2006). Outside the homeland area, Lebanon and the Anti-Lebanon, the steppe

areas of the Negev and Sinai, and the western margins of the Syro-Arabian desert in the east accommodated small mobile Natufian groups or task groups competing with other contemporary foragers.

Natufian sites are rarely larger in size than 1,000 m² and represent the occupation of a small local band who were probably kin-related (an extended family?). Dwellings are rounded pit-houses (about 3–6 m in diameter), with foundations of undressed stones and upper structures of brush and wood, probably incorporating the use of cereal straw (Valla *et al.* 2007).

Excavations of most Natufian hamlets or smaller sites have revealed the stratified rebuilding of pit-houses, burials (some decorated although not during the Late Natufian), the presence of abandoned and broken heavy mortars, pestles, bowls, cupholes, and major garbage accumulations with plenty of lithics and bone objects, body decorations, and a moderate amount of animal bones, all of which indicate repeated abandonment and re-occupation. These Natufian sites show a pattern of either sedentism or semi-sedentism testified for by the presence of commensals (sparrows, mice, rats, lizards, and foxes) first noticed by the late E. Tchernov (1984, 1994) and supported by a combined genetic and morphological study of the rodents (Auffrey *et al.* 1988). Even if the occupations of Natufian sites did not last throughout the full year, semi-sedentism can be inferred from habitation during 5–8 months a year. Despite expectations to the contrary, storage installations are rare or absent – the parsimonious explanation for this would be that hanging baskets were used instead.

Hints concerning Natufian social organization are gained from several discoveries. A large semi-circular underground building, probably for small group gatherings (closed meetings of males for feasting shamanistic activities?) was uncovered in Eynan (Ain Mallaha; Valla 1991). Additional evidence for the spiritual aspects of Natufian life include the small built-up oval rooms inside Hayonim Cave with a host of graves and incised limestone slabs, incised large slabs uncovered at Wadi Hammeh 27, and several figurines of animals and a few humans. The most striking discovery is a burial of a crippled woman, thought to be a shaman, with a huge number of tortoise carapaces, in Hilazon Cave (Grosman *et al.* 2008).

In early excavations of Natufian sites (1928–1966), flotation and systematic sieving was not practiced. Dry sieving with fine mesh (2–3 mm) was begun in the 1940s by M. Stekelis (Hebrew University) and since 1967, recovery techniques have employed flotation and fine mesh water sieving but still failed to retrieve sufficient quantities of floral remains. In several cases the few recovered grains were AMS-dated to recent periods. The poor preservation of plant remains in Natufian cave and open air sites in the southern Levant resulted from the nature of the prevailing *terra rossa* soils in these sites and unstudied diagenetic processes. Better preservation was attested in Dederiyeh cave, Mureybet, and Abu Hureyra, the northern Late Natufian sites.

Tools such as sickles, mortars, bowls, and pestles are interpreted as evidence for the harvesting and processing of cereals and legumes as food. The few recovered seeds from Early Natufian sites indicate that cereals, legumes, almonds, acorns,

pistachio nuts, and other fruits were gathered. Good bone preservation illustrates the hunting of gazelles as well as other game, and the trapping of smaller species such as tortoise, partridge, and hare. In the coastal ranges, deer, cattle, and wild boar were common, while in the steppic belt equids and ibex were typical prey. Waterfowl formed part of the Natufian diet, especially in sites along the Jordan Valley, where both migratory and nesting ducks were trapped during winter, which was a stress season. Fresh water species of fish were caught seasonally in Lake Hula, while fishing seems to have been less important along the Mediterranean coast. However, marine shells were extensively collected along the shores and perhaps from the sea (Bar-Yosef Mayer 2008).

The climatic crisis of the YD, recorded in deep-sea cores and speleothems (c. 12,900 to 11,600 BP), caused the bearers of the later phase of the Late or Final Natufian groups to disperse and become more mobile. In the Negev and northern Sinai their efforts to adapt to the new conditions through increased mobility led to the formation of an entity named the Harifian culture (Goring-Morris 1991). The collapse of the Natufian seems to have been due to the inability of the semi-sedentary modes of production to cope with the need to minimize risks to a growing population, particularly in the marginal steppic and terebinth-almond woodland belts.

A different socio-economic solution emerged in the eastern Taurus and Zagros foothills. The open-air site of Hallan Çemi Tepesi (12,100–11,200 BP), located on the bank of a tributary of the Tigris River, is a sedentary village that was established in order to control and defend the resources in that particular valley (Rosenberg 1999). Contrary to the expectations there is no evidence for the exploitation of cereals at this site, indicating that the distribution of einkorn did not reach this area during the YD (Savard *et al.* 2006).

The excavations of Zawi Chemi Shanidar and Shanidar cave layer B (c. 11,000–10,200 BP) in the Zagros testifies for the presence of groups who shifted from more mobile hunting and gathering to semi-sedentary settlements. Their rounded pit-houses do not differ from those of the Natufian, but their material culture and the few available ¹⁴C readings indicate contemporaneity with the period known in the Levant as the Pre-Pottery Neolithic A (PPNA).

2 The earliest Neolithic villages

The Neolithic Revolution (i.e., intentional cultivation of wild cereals) was probably begun during the closing centuries of the Younger Dryas, either by the Late Natufians or by contemporary foragers along the Upper Euphrates river valley (e.g., Willcox *et al.* 2009). One may hypothesize that the population that took this crucial step had previously survived partly on the exploitation of natural stands of cereals (Hillman and Davies 1992, Hillman 2003). With the continuing cold and dry conditions, C3 plants, including cereals, decreased their spatial distribution, and this apparently resulted in declining yields of einkorn, emmer, rye, and barley

in their particular natural environments. Witnessing this decline and having, like all foragers, intimate knowledge of plants' life cycles, the people had to make a social decision. The options were (1) increase mobility in order to search for resources, (2) increase the degree of sedentism in order to defend local resources, (3) move into richer neighboring territories with the risk of physical conflicts with people over there, or (4) cultivate locally available annual plants in naturally wetted soils such as alluvial fans, river overbanks, or shallow lakeside shores. In addition, as marginal areas became drier, it is expected that kin-related groups relocated, thus causing population densities to increase within the fertile, coastal hilly belt of the Levant that was also the natural habitat of the cereals. It is probably sufficient that the decision to start cultivating and its ensuing success within a few years occurred at one site, given the close communication with other groups (forming an ethno-linguistic entity); the simple technical modes of operation spread rather fast. Beyond the main distribution of one kind of wild cereal species, the same approach, intended to improve food supplies, spread to other areas of the Levant. Even with the best dated and calibrated AMS readings of charred seeds it is difficult to point to the place of origin, unless the excavated sites are farther removed from the core area and thus produce dates of a few centuries later.

Interestingly, a change in food preparation techniques took place during this transitional period. The grinding tools reflect a shift to early Neolithic food processing, as yet not fully understood. Instead of the Natufian mortars, flat grinding stone tools, which had already been employed in the northern Levant (Moore 2000), herald the new type of processing. The use of flat rocks for grinding resembles what has been found earlier at Ohalo II, and flat grinding slabs are the most common type used among Chinese Terminal Pleistocene foragers (see below).

The early phase of the Neolithic Revolution (11,600/500 to 10,500 BP), also known as PPNA, provides evidence at most sites for the cultivation of a selection of the "founder crops" (e.g., Lev-Yadun *et al.* 2000, Zohary and Hopf 2001, Willcox 2005, Brown *et al.* 2008, Willcox *et al.* 2008, 2009). The most prominent and successful were einkorn and emmer wheat, barley, and the legumes. According to the authorities at least a thousand years or more were needed for the "domestication syndrome," which incorporates among other traits a tough rachis instead of a shattering one, loss of grain dispersal aids, an increase in grain size, etc., to take over the entire fields (Kislev 1997, Tanno and Willcox 2006, Feldman and Kislev 2007, Fuller 2007, Brown *et al.* 2008). Second were the legumes, which during domestication lost their traits of dormancy and dehiscent pods (Abbo *et al.* 2008). PPNA villagers also planted and tended fruit trees such as figs (Kislev *et al.* 2006). Maintaining and propagating specific wild fruit trees is a technique recorded among recent foragers in both Africa and South America.

The fields were probably around the villages, as most are located near lake shores, on overbank deposits of rivers, and in particular on alluvial fans. The inhabited areas varied from 1.0 to 2.5 hectares with dispersed dwellings. The foundations of the rounded-oval houses, partly dug into the ground, are lined with stones.

The walls were built as a series of plano-convex mud bricks, and had flat roofs supported by wooden posts. Such buildings required a major investment when compared with their Natufian ancestors. The large villages each accommodated a fully viable biological social unit (Bar-Yosef and Belfer-Cohen 1989, Bar-Yosef 2008) and thus could determine the size of their controlled territory, but did not avoid splitting due to “scalar stress.”

Farmers as hunters are known historically and ethnographically. It is a strategy embedded in the life ways of semi- and fully sedentary cultivators and even agropastoralists. PPNA farmers continued to operate as hunters from their base-villages, probably organized by members of kin-related groups. They hunted and trapped almost the same species as their Late Natufian predecessors. In addition to mammals such as gazelles, onagers, aurochs, wild goats and sheep, wild boar, and foxes, they collected reptiles, waterfowl, and some fish. An increase in catching waterfowl was demonstrated (Tchernov 1994) and could be explained, in part, as an increase in demand not just for meat but especially for feathers. Trapping birds was easier in river valleys, near fresh water bodies in closed basins, either along the Jordan Valley or in several shallow lakes or ponds across the eastern plateau. These temporary ponds were formed during the climatic improvement following the termination of the Younger Dryas. The Levant is on the main annual routes of migratory birds between Europe and Africa. Thus, for example, the inhabitants of Netiv Hagdud, Gilgal, and Hatoula were able to exploit these seasonal resources (Tchernov 1994).

Given the size of the newly formed communities, a different pattern of territoriality emerged. There is no equivocal evidence for continued residential mobility as suggested for the Natufian population. Neolithic villages are ten times larger than the Natufian hamlets and allowed their inhabitants to keep their biological viability by having the mating system in place. The increase in the number of people was the unconscious result of becoming cultivators with permanent supplies of staple food that facilitated the weaning of newborns and their survival. The process caused settlements to have populations of 300–400 people living contemporaneously in the same location. The often numerous radiocarbon dates from these sites facilitate the calculation of the rate and tempo of garbage accumulation of reworked ashes, fire-cracked rocks, discarded mud bricks, lithics, and animal bones. Most villages survived for no more than 200–400 years based on calibrated radiocarbon dates for various sites, and were then abandoned. A detailed discussion of the reasons for abandonment is beyond the scope of this paper, but epidemics, soil erosion, soil salinization, environmental deterioration due to minor climatic fluctuations, and group conflicts come to mind.

Architectural remains of PPNA villages provide room for speculation concerning their social organization. The building of the tower and walls in Jericho, and the underground “kivas” in Jerf et Ahmar and Mureybet, could indicate the presence of a suite of local temporary chiefs or a few Big Man personalities, who could initiate the construction of public installations. Such buildings served to guard the identity of the social unit, whether for practical or for symbolic

purposes (Stordeur and Abbés 2002) and testify to a higher level of social organization beyond the Natufian band. The “kiva-type” resemble the Natufian public structure at Eynan (Ain Mallaha; Valla 1991) and may indicate a cultural continuity from the Natufian through the PPNA period to the Pre-Pottery Neolithic B (PPNB) (Cauvin 2000, Stordeur and Abbés 2002). During the PPNA, beliefs were expressed in domestic rituals and in objects passed through family ties, such as female and some male figurines. These mark a major change from the Natufian foragers’ society, where animal depictions were the majority and only rare schematic representations of humans were available (Kuijt 2000, Gebel *et al.* 2002 and papers therein).

It is therefore hypothesized that, similarly to changes known from the history of technological revolutions, the onset of cultivation by the villagers resulted in numerous social changes (e.g., Bar-Yosef and Belfer-Cohen 1992, Cauvin 2000, Bellwood 2005). Most probably women, who were the main plant food collectors, became the ones who initiated cultivation, and there is little doubt that they worked in the fields and in domestic contexts. Indeed, we must note the shifting roles of males and females within the farming communities. Women and children gathered wild plants, fruits, and slow-moving reptiles such as tortoises and lizards from around the village, while males continued to hunt away from camp. We assume that males were possibly involved in preparations for cultivation, such as felling trees, tilling small plots with hand picks, building fences, and the like. In addition, females were responsible for food processing. Grinding and pounding require continuous energy expenditure. This contention of increasing workloads of females is based on ethnographic examples and has been backed by skeletal studies (Molleson 2007).

Kuijt (2002) proposed that in the early villages the drive to maintain an egalitarian society motivated changes in mortuary practices. However, the building of communal structures such as the tower in Jericho or the “kiva-type” buildings in Jerf et Ahmar and Mureybet, as well as the emerging social complexity already seen in the early PPNB, indicate that PPNA communities were not egalitarian. Every social unit of 250–400 people, with its own scalar stress, required leaders to avoid anarchy and maintain social order. Splitting from the community, as much as increase of local population, resulted in the establishment of new villages.

3 Emerging social complexity in the Levantine Neolithic

The villages of the PPNB period (c. 10,700/500 to 8,400/200 BP) are larger than the earlier PPNA ones and the common dwellings are square or rectangular, with flat roofs and in some cases, in late PPNB buildings with two floors were constructed (e.g., Basta, southern Jordan). Plaster produced from burned limestone or gypsum lined the floors and lower parts of the interior walls. In a few villages, such as in Bouqras, situated at the confluence of the Khabur and the Euphrates rivers, the formation of compounds with several rooms resemble the

density and closeness of houses in Asikli Hüyük and Çatalhöyük on the Anatolian plateau. Such over-crowded human agglomerations raise again the issues of territorial defense and expression of ownership.

A major transformation in the exploitation of animal resources had already begun during the Early PPNB (EPPNB) (*c.* 10,700/500 to 10,000 BP) in the Taurus foothills. The process of husbandry started with sheep and goats (Zeder 2006, Vigne 2008), and is currently supported by DNA studies of modern goats. During the middle and late PPNB (*c.* 10,000 to 8,200 BP) goats and sheepflocks were brought into the central and southern Levant, possibly along the same exchange routes that channelled the Anatolian obsidian, and chlorite bowls, southward and Red Sea marine shells northward (e.g., Bar-Yosef Mayer 2005). The best example for the translocation of goat, sheep, cattle, and pigs (as well as fallow deer and, later, dogs and cats) is documented in the Cypriot PPNB site of Shillourokambos (Vigne and Cucchi 2005). These animals, not native to the island, had to be transported on sea craft by colonizing farmers. In the semi-arid sites of the Syro-Arabian desert, goats did not become part of the economy until 8,000/7,500 BC or later. Cattle herding during this period produced ample evidence of the use of milk (Evershed *et al.* 2008).

Indeed, the Early and Middle PPNB farming communities provide evidence for the full set of agricultural activities, such as sowing fields with cereals and harvesting, and growing legumes, including chickpeas and broad beans. Flax was grown and used for manufacturing fibers, instead of collecting it in the wild, and this caused a change in clothing, the use of cords, and the like (McCorriston 1997). There is also evidence of herding goats, sheep, and cattle, as well as breeding pigs. Successful farming was supported by a higher annual precipitation than today, as recorded in the speleothems (Bar-Matthews *et al.* 1999; Figure 3.2). Analyzing the stable carbon isotopes of seeds from PPNB contexts in Tell Halula, on the Euphrates in Syria, led Araus *et al.* (2001) to suggest that the crops enjoyed better water supplies and produced higher yields than those grown in the same area today. The fields were either fed by winter rain or by irrigation (van Zeist 1986).

Among the toolkits there are differences between the northern and southern Levant. In the latter, tools were bifacially shaped with transverse blows producing a sharp cutting edge (Barkai 2005), while in the northern Levant and Anatolia, axes-adzes were fully polished. These tools were employed in tree-felling, wood-working, crafting objects and shaping posts, and building sea-craft. Harvesting equipment included simple sickles, V-shaped bone tools for stripping the seed heads from straw, and later the threshing board or *tribulum* (Anderson 1998). Arrowheads proliferate during this period (Gopher 1994), and while yields from game animals decreased, the large number of projectiles may reflect the increase of warfare among Neolithic tribes.

Storage facilities include special built-in installations and small rooms in houses or courtyards. Changes in the sizes and locations of storage facilities mark the shift from nuclear family consumption to larger social units and perhaps, already in some PPNB sites, to an institutionalized control of public granaries.

In sum, the fully developed Neolithic economy, with its domesticated species of plants and animals, seems to have emerged earlier in the northern Levant. Due to geographic proximity and the exchange of obsidian, chlorite objects, and sea shells, innovations in the north did not escape notice by the inhabitants of the central and southern Levant, and the resulting regional network formed the PPNB interaction sphere (Bar-Yosef and Belfer-Cohen 1989).

The social changes are best observed in several major sites. In each of these settlements the archaeological contexts reflect both domestic and ritual activities, forming a continuum from the sacred to the mundane. Buildings that served as shrines are recognized in sites where large excavated exposures were made, or in particular, if the edge of the village was uncovered. Examples include Çayönü, Nevali Çori (Hauptmann 1999), and Beidha (Byrd 1994, Özdoğan 1999). Other sites where ritual functions override the remains of daily activities are Kefar HaHoresh (Goring-Morris 2000) and probably Bajja (Gebel 2002). But undoubtedly the most impressive site is Göbekli Tepe (Peters and Schmidt 2004, Schmidt 2006). The large polygonal buildings in the lower layer of this site and the rectangular buildings above, with their T-shaped carved pillars, many of which bear reliefs of various animals, reflect a significant amount of organized labor invested in building, maintaining, and refilling the structures when they went out of use. These observations raise issues of social organization, labor channelling and control, and indirectly the emerging of inequality.

Sculptures at Göbekli Tepe and Nevali Çori, as well as in the later buildings at Catalhöyük, exemplify both animal and human figures, including ithyphallic representations and the presence of raptors, with only minor appearance of female figures. The complexity of the symbols, which are not easy to decipher, could reflect the intricacies of an elaborate cosmology, but this will not be discussed here.

No less important are the caches of human plaster statues uncovered in Jericho and Ain Ghazal (Rollefson 2000). Their archaeological context testifies to the intentional burial of used cultic objects. The breakage of such holy items prior to their interment is a well-known phenomenon from the historical periods in the Near East. The plastered statues, some of which are only busts, others of which hold their hands covering the lower part of the belly, are seen as female representations. All have eyes encircled with asphalt lines and stripes of red color on their bodies. By employing an archaeological analogy to later millennia, the statues may represent a pantheon of deities, and the human figure can symbolize both a real and a mythological being. In addition, ceremonial centers or special ritual localities such as Nahal Hemar cave could have been landscape markers of kinship-based territories.

In sum, when the evidence for public ceremonial and domestic ritual activities as well as the variable mortuary practices (including skull removal of probably elite societal members and their plastering) are taken together, the comprehensive list can serve as a basis for evaluating the social complexity of the PPNB period (Bar-Yosef 2001).

Entities of foragers who continued to hunt and gather were contemporary with the PPNB agriculture-based villages, but did so while developing intricate relationships with the latter. Their mutual relationships could have ranged from friendly encounters to violent conflicts, as is well known from historical examples. These interactions played an important role, not yet fully researched, concerning the transfer of material elements and information. The archaeological example for the mutual relationships of hunters–farmers is the game drives, known as “desert kites”, which were large installations laid out by PPNB foragers to hunt gazelles or onagers *en masse*. The employment of this technique, which is also known from other regions in the world, must have meant that the villagers had the need for meat, hides, and horns from wild species and not only from their domesticated livestock.

While the evidence for physical conflicts is poor, as mentioned above, it seems likely that some degree of inter-village disagreements or warfare occurred among farming societies. The abandonment of PPNB sites could have been the result of local clashes. The proliferation in the production of arrowheads everywhere during this period when hunting had become a less important source of meat may reflect “war before civilization” (Keeley 1996). By about 9,500 BP, the economic dichotomy between farmers–herders and pastoral nomads had emerged and continued to widen in the following millennia. Physical conflicts should also be expected to have occurred, especially in bad years. Indeed, the boundaries between farmers–herders and foragers in semi-arid or mountain regions were far from stable during the PPNB.

4 The collapse of Levantine PPNB social systems

For those who refuse to believe that abrupt climatic crisis can drive sudden cultural change, the collapse of the PPNB societies in the Levant and some adjacent regions is a good example that is now accepted by more archaeologists than it was a decade ago (Bar-Yosef 2001, Berger and Guilaine 2008). The archaeological evidence is derived from stratigraphic unconformities and site abandonment as well as the recognition that only very few settlements survived over many centuries. Generally, the abandonment of a house in a living village can be accounted for by a variety of simple reasons, from the death of the head of the family to the outcome of verbal or physical conflict. However, when an entire village is deserted, the reasons could be more complex, including overexploitation of the immediate environment (an argument used in the past), societal conflict, disease, or the impact of consecutive droughts. There are only rare examples for the burning of an entire village that could be due to inter-group hostilities, such as the PPNB site of Ganj Dareh in the Zagros (Smith 1976). But the paucity of evidence does not necessarily reflect the endurance of peaceful lifeways. To interpret field observations as an overall socio-economic collapse we need first to document the timing of abandonment and to determine whether its scale was

only local or whether it represents similar desertions across an entire region. Second, we need to search for the reasons for the observable abandonment, and as in every case of a “why” question, the answer is open to several interpretations.

Abandonment is attested by stratigraphic gaps between PPNB and later layers at Çayönü, Bouqras, Beisamoun, Mureybet, Munhata, Yiftahel, Ain Ghazal, Basta, and many other sites in the Levant. The establishment of new hamlets and farmsteads further supports the idea that the villages were abandoned across the southern Levant. The new sites contained ceramics and lithic assemblages of a cultural entity called the Yarmukian. Among these the large settlement of Shaar HaGolan is composed of large compounds located near the Yarmuk River, and in spite of its situation in the bank of a flowing river, a well, perhaps for fresh water, was discovered (Garfinkel *et al.* 2006). Wells are known from PPNB and later sites in Cyprus and the coast of Mt. Carmel (Atlit-Yam), indicating that the technology for digging wells was already known earlier.

The culprit for the collapse is a relatively abrupt cold and dry period lasting a century or several centuries, and known as the “8,200 BP cold event” (Alley *et al.* 1997, Bar-Yosef 2001, Berger and Guilaine 2008). The Late or Final PPNB sites featured complex tribal societies subsisting on farming and herding, without centrally controlled granaries, and in which demand by better-off individuals drove the flow of foreign commodities. However, under the worsening environmental conditions, these societies could not continue to accumulate surplus. A shift in the pattern of seasonal rainfall resulted in lower yields for summer harvests and forced the inhabitants to search for pastures for their herds further away from the villages. The economic deterioration resulted in a societal change, which archaeologically is expressed in the disappearance of the previously large villages and the establishment of smaller villages or hamlets. The new conditions probably enhanced the reliance on the more flexible subsistence strategy of pastoral nomadism; however, a detailed discussion of these cultural changes is beyond the scope of this chapter.

Similar impacts of climatic fluctuations in China on past societies of hunter–gatherers and farmers are evidenced in the archaeological records accumulated over the past decade. Before delving into a discussion of climate change and the reconstructed cultural evolution in this vast landmass, we need to review its roots during the Late Pleistocene.

5 The transition from foraging to farming in China

In comparing the processes that led to the establishment of farming at the two ends of Asia, we need to take into account differences in geographic scale and climatic conditions. Currently available archaeological and palaeoclimatic evidence may indicate that the emergence of cultivation of cereals in the Levant, and possibly in North China, occurred at the end or immediately after the YD. Cultivation of wild rice was initiated in South China either during the same

millennium or later. The detailed archaeological sequence is more poorly known in China than in the Levant due to the immense territory of this country and fewer excavated and dated sites. However, recent local and regional reviews provide summaries of the known archaeobotanical and archaeozoological records, as well as the ongoing debates concerning their interpretations (e.g., Cohen 1998, 2003, Zhao 1998, 2004, 2005, Lu 1999, 2002, 2006, Shelach 2000, Yuan 2002, Bellwood 2005, Crawford *et al.* 2006, Bettinger *et al.* 2007, Flad *et al.* 2007, Fuller 2007, Fuller *et al.* 2007, 2009, Lee *et al.* 2007, Liu *et al.* 2007, Zheng *et al.* 2007, Yuan *et al.* 2008, Zhang and Hung 2008, Crawford 2009).

In spite of these limitations, comparing the wealth of Chinese site size, architectural remains, burials, pottery, stone tools, early appearance of jade, and other cultural markers, with the Levant, can tentatively provide us with ideas as to how to disclose the nature of socio-economic processes during the Terminal Pleistocene and Early Holocene in China. In addition, we should be aware of the difficulties in employing the small number of radiocarbon dates from most of the sites. Wood was used for construction of the early rounded and oval pit-houses as well as the square or rectangular buildings of the following millennia. The paucity of AMS dates of short-lived samples as seeds may result in adopting long time spans for village sites that survived over just a few centuries.

Before delving into the socio-economic changes in North and South China it is important to stress the role of rivers across this landmass. The numerous rivers, mostly with a very low gradient (even during the glacial periods when sea level was lower) were the easy routes for communication over large distances. The knowledge of navigation has an old history in Southeast and East Asia. The colonization of New Guinea and Australia by modern humans was achieved by seafaring peoples some 45 ± 5 ka BP. Both riverine and coastal navigation had thus been a viable option since the early Upper Paleolithic. Direct evidence for river transport has been uncovered in waterlogged sites such as Kuahuqiao (c. 8,000–7,300 BP) where a canoe and several paddles were found (Zhejiang Institute of Cultural Relics and Archaeology 2005). One can safely assume that remains of river or sea craft of different types will be exposed in other waterlogged Late Upper Paleolithic or Early Neolithic deposits. Relatively rapid and constant long-distance connections are assisted by interpretations of cultural similarities, such as pottery types, across China (e.g., Chang 1986, Cohen 2003).

Hence, in the following pages I will briefly review the available archaeological evidence from North and South China on the background of past climatic conditions within a framework of a hypothesis that derives its foundations from the Levantine sequence discussed above.

Palaeoclimatic data in China is often obtained from cave speleothems, lake and marine pollen cores, as well as loess sequences. The Last Glacial in China was characterized by significant and frequent oscillations, well recorded in a suite of proxies such as the Himalaya ice cores, loess sediments, pollen cores, marine cores, and cave speleothems (e.g., G. Yu *et al.* 2000, Lin *et al.* 2007, Cosford *et al.* 2008, C. Yu *et al.* 2008). Among the eastern sites, Hulu cave,

near Nanjing (Wang *et al.* 2001), produced a long palaeoclimatic curve that best fits the GISP2 ice core. Other caves include Dongge (Dykoski *et al.* 2005), Heshang (Hu *et al.* 2005), Qingtian (Liu *et al.* 2008), Sanbao (Wang *et al.* 2008), Songjia (Zhou *et al.* 2008), and Timta in Tibet (Sinha *et al.* 2005). These sources indicate a general contemporaneity with climatic changes recorded in the Greenland ice cores. The LGM was cold and dry followed by slow rising temperatures and increasing rainfall resulting from both Pacific and Indian Ocean monsoons. An additional amelioration during the Bølling–Ållerød improved the conditions in northern China with rainfall brought by the westerlies. These shifted anew during the YD as both terrestrial sources and marine pollen rich in *Artemisia* sp. (Yi and Saito 2004), carried by the Yellow and Yangtze rivers, demonstrate a return to colder and drier conditions. Increasing wetter and warmer climate marked the onset of the Early Holocene (e.g., Liu *et al.* 2008).

6

North China

The LGM conditions in North China were cold and dry except for a few protected habitats (G. Yu *et al.* 2000, Wünnenman *et al.* 2007), but by c. 16 ka BP climatic amelioration was witnessed in the slowly rising temperatures, increasing rainfall, and a moderate return of forests habitats to the loessic areas, judged from the evidence for the earliest Holocene (e.g., Ren and Beug, 2002). As the monsoon system became stronger and penetrated further north, particularly during the Bølling–Ållerød (B/A, c. 14.5 to c. 13/12.8 ka BP), it facilitated the spread of foragers within this region.

Several researchers have provided information concerning the environmental conditions that facilitated the growth of human populations, producers of the microblade industries, prior to the YD (e.g., Bettinger *et al.* 2007, Chen 2007, Wünnenman *et al.* 2007). Most sites from this period are small, ephemeral and reflect varying degrees of mobility. Series of such occupations with microblade industries have been sampled and studied (Chen 1984, Lu 1999, Cohen 2003, Chen 2007, Kuzmin *et al.* 2007 and papers therein).

Xiachuan (Figure 3.3) is one of the important sites where a few radiocarbon dates indicate the presence of at least two major occupations rich in microblades (c. 25 ka and 15 ka BP) and a large number of grinding slabs (Lu 1999). Lu (2002) reports siliceous sheen on several flakes that resemble her experimental pieces employed in harvesting foxtail grass panicles. Another multi-layer site is Shizitan, where occupational horizons were interspersed with loess accumulations over several meters thick (Shizitan Archaeological Team 2002) dated to c. 20 through c. 11 ka BP. On the whole, microblade industries occur at several hundred sites across North China, southern Siberia, Korea, and Japan (Chen 2007, Kuzmin *et al.* 2007, Kajiwarra 2008). Flat or slightly concave grinding stones and rubbing stones are a common component in these sites, indicating small seed grass



Figure 3.3. The location of the Late Upper Paleolithic and Neolithic sites in China mentioned in the text.

processing. In addition several species of deer, equids, wild boar, and a few carnivores were ubiquitous in this region (e.g., Flad *et al.* 2007).

It seems that the penetration of the westerlies during the B/A increased the potential for hunter–gatherers to expand their populations into previously arid or semi-arid habitats in Western China. Thus, the abrupt change to the YD conditions (e.g., Liu *et al.* 2008) around 12,800/500 BP that lasted until 11,700/600 BP was a major disaster. The sudden increase of dryness across North China may have caused the same reactions as observed in the Levantine arena. Hunter–gatherers retreated to more favorable habitats, possibly in South China (Bettinger *et al.* 2007), and perhaps established a few sedentary communities within the region in protected river valley and lakeside locales. Increased exploitation of resources by intensification could have been the result of sedentism and reduced mobility that resulted in “population pressure” and increased competition for resources. Hence, during the YD and the first two millennia of the Holocene (11,500 to 9,500 BP) we note the appearance of larger sites as agglomerations of people (families and sub-clans?), reflecting the need for security and territorial defense, whether in view of real or imaginary enemies (Roscoe 2009). Sites such as Donghulin, Nanzhuangtou, Zhuannian, and Yujiagou date to either the very late YD and Early Holocene, their occupational surfaces range from several hundred to several thousand square meters and in addition to rounded pit-houses they contain a mixed core and flake industries, sometimes with microblades as well as pottery. Nanzhuangtou (Hebei, Figure 3.3), a lakeside village, did not contain a microblade assemblage but had a rich bone and antler toolkit, pottery, and the evidence for hunting of several species of deer, dog, wild boar, wolf, and chicken and gathering soft-shell turtle and shellfish (Underhill 1997, Cohen 2003). Only the recovery of plant remains by flotation will clarify whether late foragers in the North were only collectors or also part-time cultivators growing either broomcorn and/or foxtail millet.

The next phase is represented by the cultures or sub-cultures of Huoli, Cishan, and Peligang, as well as the outliers of the Xinglongwa sites in Inner Mongolia and Dadiwan and its contemporaries in the Laoguantai culture area in the west. Sites in these culture areas emerged as cultivators of millet within the Yellow and Wei River basins (Zhao 2004, Crawford *et al.* 2006, Lee *et al.* 2007, Barton *et al.* 2009, Crawford 2009, Lu *et al.* 2009). It seems that these were the originators of dry farming broomcorn and foxtail millet farming (Zhao 2004). One may suggest that the three sub-cultures are the primary “core area” where cultivation of wild millet species was established, and by definition, those who cultivate plants annually are identified as “farmers”.

The first farming communities are characterized by a surface of *c.* 1–2 ha in size, with semi-subterranean rounded and the first square houses, a large number of storage pits, some containing abundant cereal grains and others that are interpreted as of ritualistic use, distinct cemetery areas, abundant pottery, stone adzes, axes, spades, and four-legged grinding stones, best known from Cishan.

A new study of plant remains from Cishan suggests that broomcorn millet (*Panicum miliaceum*) was first cultivated/domesticated by c. 10,300–8,700 BP (Crawford 2009, Lu *et al.* 2009). However, the earliest radiocarbon dates in the list of Lu *et al.* (2009) is still highly debated (Z. Zhao, personal communication). The presence of the two domesticated varieties of millet, *Panicum miliaceum* and *Setaria italica*, in Xinglonggou (Xinglongwa culture) and Peiligang cultural contexts from c. 8,000 BP, as well as at the site of Dadiwan (7,800–7,300 BP) indicate a long period of cultivation of wild crops before the full dominance of domesticated cultigens was reached. If additional evidence will verify the impact of the YD on foragers who intensified food acquisition by initiating cultivation, we can then establish an interesting coincidence between North China and the Levant.

The option of quasi-contemporaneity between millet cultivation in North and rice in South China is indicated by flotation samples from the Houli culture site, Yuezhuang (Jinan, Shandong). With one AMS date of 7,900 BP the presence of 40 broomcorn and one foxtail millet seeds, along with 26 rice seeds, are considered as indicating an unexpectedly early arrival of rice in the Yellow River area (Crawford *et al.* 2006). Additional support for early presence of rice in the Yellow River area is the Jiahu (Peiligang culture), where remains of other plants, such as *trapa* and wild soybeans, were found. Like many sites of this culture, dwellings were rounded pit-houses, rich in pottery, with special discoveries such as barbed spear heads, needles, and flutes (Zhang *et al.* 2004). The fauna includes domesticated dogs and pigs as well as cattle (possibly wild), deer, and fish.

Fish are relatively scarce in the Yellow River (when compared to the Yangtze River), so it is not surprising that the few detailed studies of North China faunal assemblages (Yuan and Flad 2002, Flad *et al.* 2008, Yuan *et al.* 2008) document an abundance of nondomesticated terrestrial species such as deer and several carnivores including wolves, the foremost hunted game being wild boar. Pigs were the first to be adopted by farmers who continued to hunt. The process, possibly similar to the one in the Levant, began with “cultural control” of individuals attracted to the garbage dumps of villages, at least by 8,000 BP. By 6,000 BP pig meat had become dominant: 60% of consumed mammal tissues (Yuan *et al.* 2008).

The Xinglongwa culture in Inner Mongolia and Dadiwan in the Laoguantai could be considered as “secondary centers” into which millet cultivation expanded (Bettinger *et al.* 2007, Barton *et al.* 2009). Flotation samples from the Xinglonggou site uncovered many thousands of carbonized seeds, mostly of wild grasses, with 1,500 of broomcorn millet and fewer than 100 of foxtail millet (Zhao 2005). This discovery lent support to the suggestion by Shelach (2000) that millet cultivation started earlier than the Xinglongwa culture sites.

The well-ordered rectangular–square houses in Xinglongwa (Yang *et al.* 2007; Figure 3.3), all oriented in the same direction, attached or close to one other, demonstrates a well-organized agricultural village of 2.3 ha in size, with clear hints of social hierarchy represented by a central house and a burial with jade earrings. The ditch surrounding the village, on top of a low hill, could have been used to collect rain water, but was probably meant to physically and/or symbolically deter

real or imaginary enemies. Warfare among agricultural societies is a well-known phenomenon (e.g., Keeley 1996). If long-distance similarities are meaningful, then the arrangement of the houses at Xinglongwa resembles sites like Asikli and Çatalhöyük in Anatolia that belong to the second phase of the Neolithic Revolution in the Levant. Assuming that this is also true for China, then it supports the proposal that millet cultivation had already been practiced in this region for some 2,000 years.

In sum, while we still do not have the full information on when and how cultivation of wild millet started, once it was done, and as the plants became domesticated, accompanied by raising pigs, dogs, and later other domesticated species, the villages increased in size, reflecting population growth. For several millennia the Early and Middle Neolithic sites of North China were larger than their contemporaries in South China. A major change was caused by “the 8,200 BP cold event” already indicated by ample evidence, but discussion of this topic is beyond the scope of this chapter.

7

South China

The late Upper Palaeolithic in South China, the vast region from the Qinling Mountains and the Huai River to the southeastern coast, produced numerous assemblages that preserved the old tradition of cobble-tools such as choppers, cores, and flakes, small cupholes on cobbles, perforated cobbles, and a few bone, antler, and shell tools. This region produced the earliest evidence for making pottery: *c.* 18/17,000 BP in Yuchanyan cave (Hunan); Xianrendong and Diaotonghuan in Jiangxi, and Miaoyan (Guangxi) (MacNeish *et al.* 1998, Zhang and Hung 2008, Boaretto *et al.* 2009). Phytoliths from the deep sequences of Xianrendong and Diaotonghuan indicate the exploitation of rice (Zhao 1998). A marine core removed at the edge of the Late Pleistocene Yangtze delta demonstrated the lack of rice phytoliths during the YD (Lu 2002). Carbonized seeds from securely dated assemblages did not support the suggestion, based on phytolith forms, that rice was domesticated prior to the YD.

Recent excavations at Yuchanyan cave produced additional data concerning the pre-YD period. A series of occupations interspersed by several gaps, dated from *c.* 18,000 through 13,800 BP, were recorded at this site. The remains of two pots found in the deposits of the “lower midden” are dated to *c.* 18,000–17,500 BP. Most of the ash lenses of the “upper midden” deposits (0.8–1.5 m thick) accumulated rapidly from 14,500 through 13,800 BP, marking the onset of the Bølling–Ållerød warmer and wetter period that is well recorded in the Chinese speleothems (e.g., Wang *et al.* 2001, Dykoski *et al.* 2005). The exposed thick lenses of wood ash provided quantitative evidence for the hunting and trapping strategy supplemented by terrestrial snails (*Viviparus* sp.) that when taken together with previous reports, reflects the suite of forager activities of those who camped in this small cave (Yuan 2002, Boaretto *et al.* 2009, Prendergast *et al.* 2009).

The lithic assemblage is composed of numerous choppers shaped on flat cobbles and flakes, some of which bear retouch. A few bone tools and shell objects complete the assemblage of artifacts. The animal bones consisted mainly of several deer species of all sizes, from the small deer (< 25 kg) including *Hydropotes* sp. (water deer), *Muntiacus* sp. (muntjak), and *Moschus* sp. (musk deer), to medium-sized deer (25–100 kg) *Cervus nippon* (sika deer), and the large ones, namely, *Cervus unicolor* (sambar) and *Elaphurus davidianus* (Père David's deer) that weigh more than 100 kg (Prendergast *et al.* 2009). Other species include macaque, hare, a variety of small carnivores, and rodents, particularly bamboo rat, as well as birds such as heron, tern, crane, goose, and others. The ducks were all wetland taxa. Fish included carp and catfish. In sum, the young age of the deer and the presence of wintering wetland birds (whose breeding grounds are in North China, Mongolia, or Siberia) indicate that Yuchanyan cave was occupied during the winter and spring months.

Xianrendong and Diaotonghuan caves (Jiangxi; Figure 3.3) are located next to each other in the general area of Lake Poyang, some 150 km south of the Yangzi River (MacNeish *et al.* 1998), where wild rice was gathered, as reflected in the phytolith assemblages (Zhao 1998). Both sites contained rich assemblages of cobble-tools, bone and antler tools (including harpoons), perforated shell objects, and early pottery (MacNeish *et al.* 1998, Zhang 1999). The faunal assemblages in both caves are similar to Yuchanyan, with a clear dominance of deer species, but it differs from Yuchanyan in that the second most abundant hunted mammal is wild boar. Wild chicken and duck were also identified among the numerous bird remains, most of which winter in this area (MacNeish *et al.* 1998).

The large number of radiocarbon dates from Xianrendong and Diaotonghuan reflect early pre-LGM occupations and the use of the caves during the LGM times (radiocarbon dates *c.* 23,000–22,000 BP), when northern China saw the outward migration or disappearance of many forager groups (Bettinger *et al.* 2007). According to the available dates the two caves were deserted and reoccupied several times and the latest occupations are dated by a few readings to 13,800–11,500 BP, the YD time (MacNeish *et al.* 1998). MacNeish's collaborative excavations project was followed by additional fieldwork carried out by a team from Peking University (Zhang 1999).

There is no recorded stratigraphic continuity between these three sites, or others that are not dated but attributed to the Late Palaeolithic, and the subsequent early villages in the middle or lower Yangtze basin. However, archaeologically there is ample material evidence of stone, bone, antler, and shell tools, as well as pottery and other stone objects (cupholes and “digging stick weights”), to indicate that local hunter–gatherers were the first to start wild rice cultivation in this region.

Pengtoushan and Bashidang, considered in the periodic subdivision as Early Neolithic, and located in the mid-Yangtze alluvial plain around Lake Dongting in northern Hunan, are among the earliest villages. AMS dates show that the time span of the two was from *c.* 9,200 through 8,000 BP (Hunan Provincial Institute of Cultural Relics and Archaeology 2006).

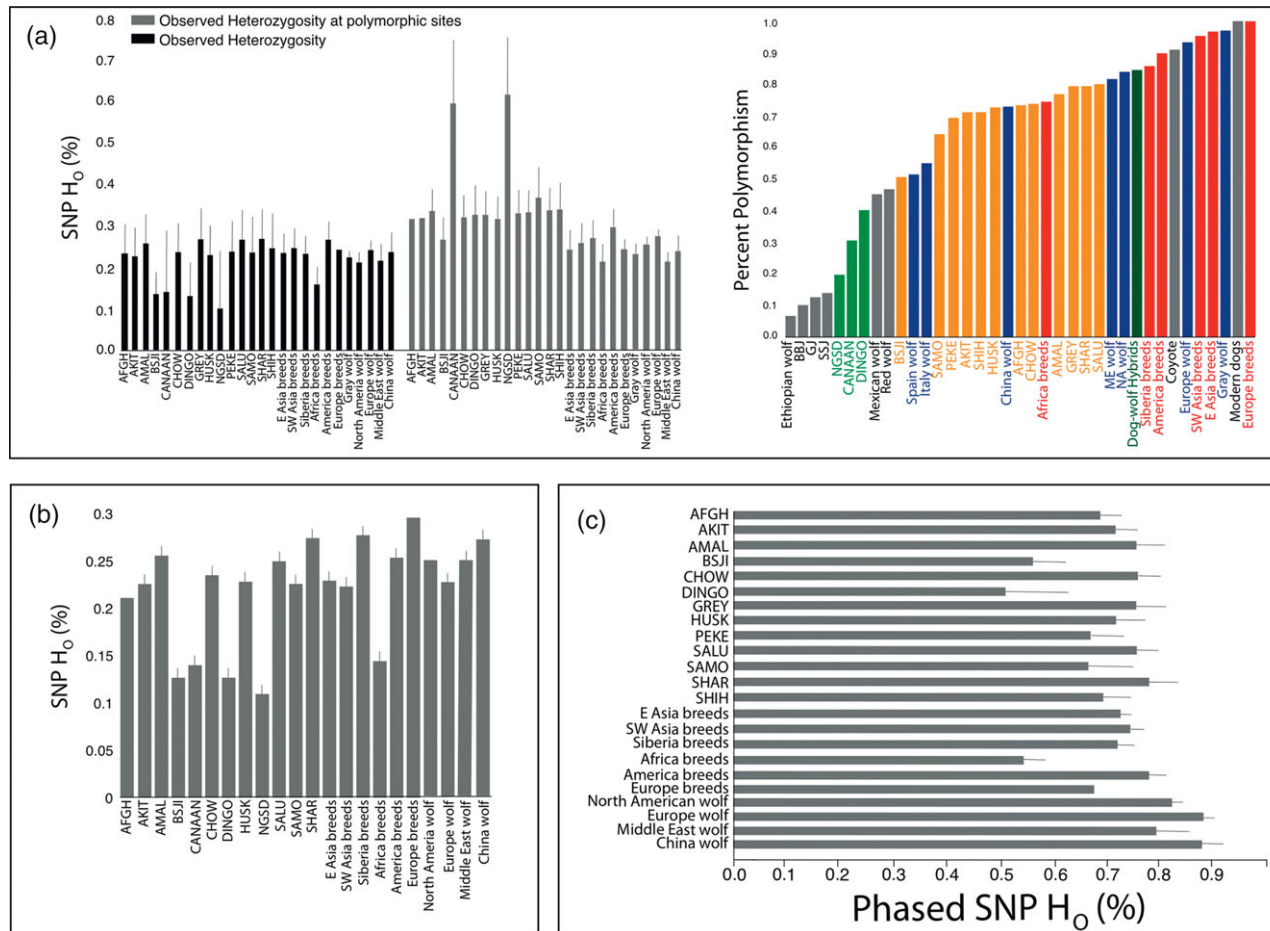


Figure 11.2. (a) Canine SNP microarray variation based on estimates of observed heterozygosity (H_0) for 48,036 SNPs and percent polymorphism for domestic dog breeds and breed groups (Savolainen *et al.* 2002), wolf populations, and canid species. (b) SNP-based estimates of observed heterozygosity for 546 SNPs ascertained from dog-wolf comparisons. (c) Observed heterozygosity (H_0) from phased genotype data. Note the higher values of heterozygosity in wolves vs. dogs as opposed to the opposite pattern in (a), suggesting the effect of ascertainment bias. Haplotype diversity estimates included breeds containing at least six individuals and wild canid populations for 500kb windows across the genome. Observed heterozygosity was estimated for 10-SNP non-overlapping windows across the genome. Modified from vonHoldt *et al.* (2010).

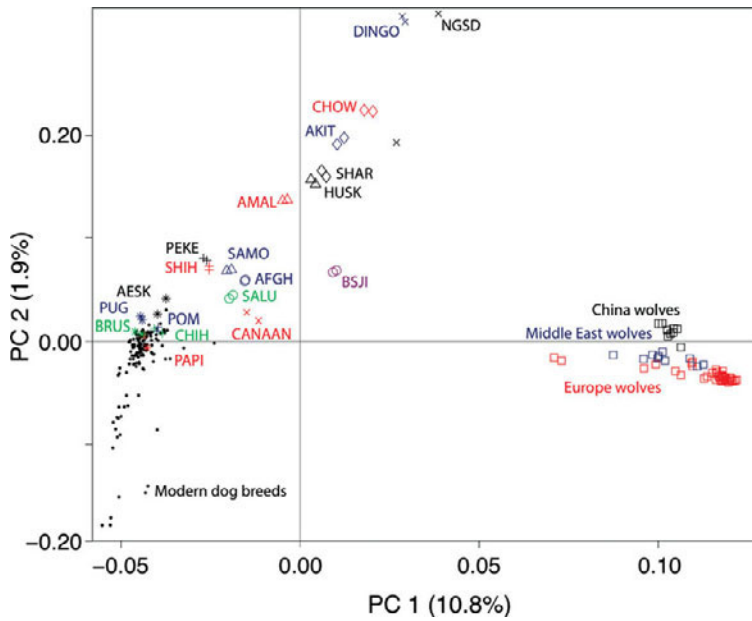


Figure 11.3. Principal components analysis of 171 dogs and 58 Eurasian wolves for 48,036 SNPs (Middle East wolf populations: India, Iran, Israel, Oman, Saudi Arabia, and Turkey). Modified from vonHoldt *et al.* (2010).

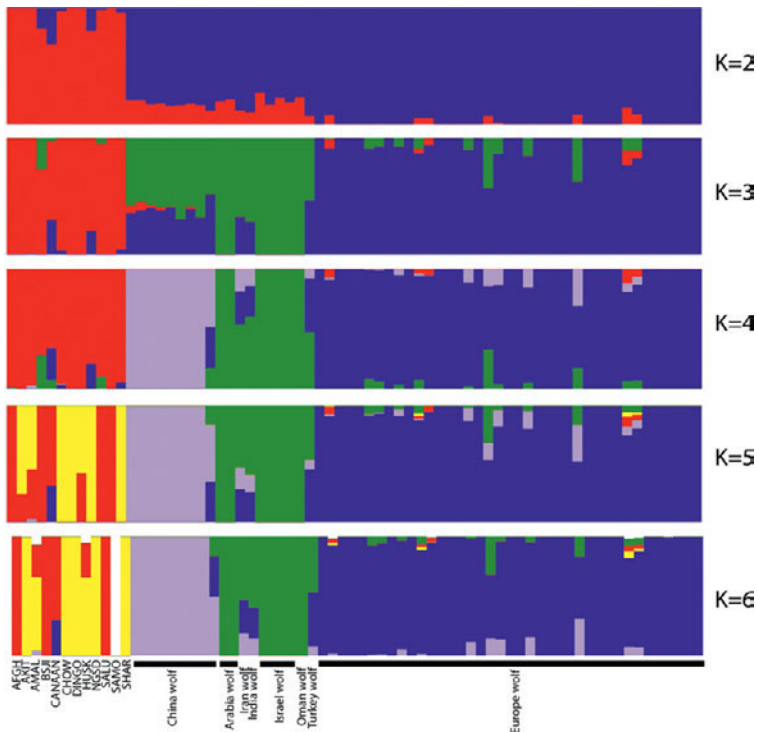


Figure 11.4. STRUCTURE analysis of ancient dog breeds (1 dog per breed) and 58 Eurasian wolves for 43,000 unlinked SNPs. The y-axis is the percent membership to each ancestral population and the x-axis is an individual multilocus genotype. (Dog breed abbreviations: Afghan Hound, AFGH; Akita, AKIT; Alaskan Malamute, AMAL; Basenji, BSJI; Canaan dog, CANAAN; Chow-chow, CHOW; Siberian Husky, HUSK; New Guinea Singing Dog, NGSD; Saluki, SALU; Samoyed, SAMO; Shar-pei, SHAR). Modified from vonHoldt *et al.* (2010).

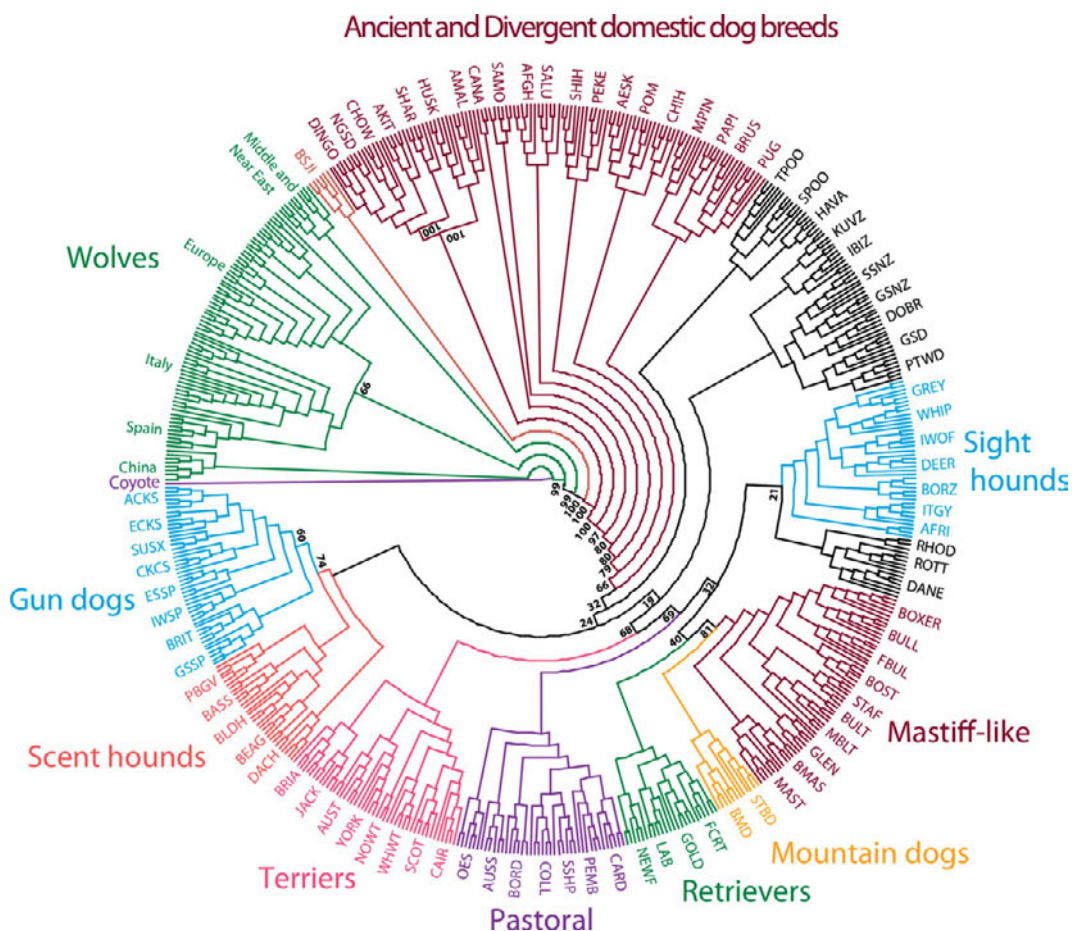


Figure 11.5. Neighbor-joining cladogram of 574 dogs and wolves, rooted with coyote data for 43,954 unlinked SNPs. Branch support for 1,000 bootstraps is indicated. Modified from vonHoldt *et al.* (2010).

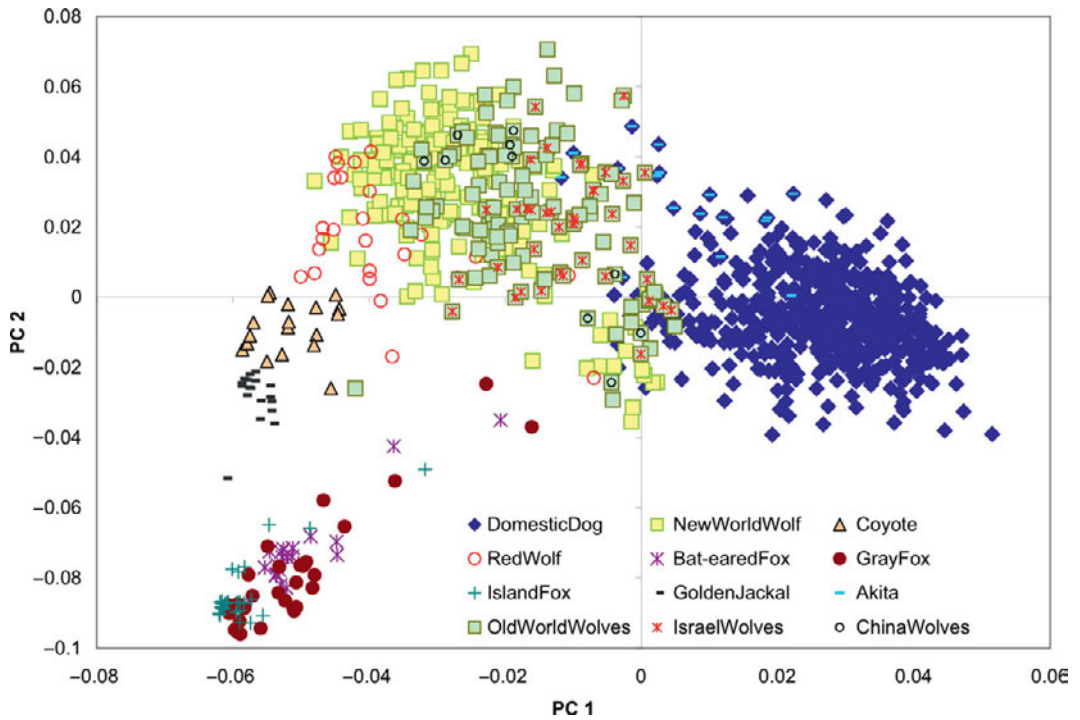


Figure 11.6. Principal components analysis of 106 SNP (dog-derived) genotypes from 18 dog breeds, 14 gray wolf populations, one coyote population, and 4 other wild canid populations. Modified from Gray *et al.* (2009).



Figure 19.1. Diversity of cocona (*Solanum sessiliflorum*) fruit size and shape has been created by selection for novel fruit types by Yanesha and other indigenous peoples of the upper Amazon (from Salick 1992a).



Figure 19.2. Species diversity in Yanéscha agriculture. (a) Over 75 species in home gardens. (b) Over 125 species in swidden fields, including species rarely grown in nonindigenous agriculture, such as (c) edible roots of the canna lily and (d) colored cotton used in traditional weaving.



Figure 19.3. (a) At Mt Khawa Karpo on the Tibetan border, gradient analysis extended from 2,000m in the Mekong River valley (lowest point in picture) to the snow line at 5,000m.



Figure 19.4. (a) Cassava varieties of the same Yanéscha were systematically sampled in 1983–86 and in 1999, 15 years later. Here, the same woman is photographed in her cassava field during the first survey (inset photo) and second survey (larger outer photo).



Figure 19.6. Tibetans recognize and respond to climate change. For example: this 85-year-old woman with her great grandson (left) voices her fears, “I am worried that the earth will be destroyed if the snow disappears completely”; offerings and prayers are ceremonially presented to *Klu*, a Tibetan water god (center), in order to control weather and disease; Tibetans adapt to climate change by growing grapes and producing award-winning ice wine (right).

Pengtoushan, situated 80 km south of the Yangtze River, is about 2 ha in size. Several oval semi-subterranean dwellings, above-ground foundations for a rectangular building (of a later phase), 21 burials, 15 pits, and a small segment of a ditch around one house were exposed (Hunan Provincial Institute of Cultural Relics and Archaeology 2006). The conditions of preservation were poor, and only a few grains of rice were found, so it could not be determined whether they are of the wild variety or already domesticated. The faunal assemblage is small but includes bird bones.

Bashidang, located in the same area, is 3 ha in size and has a ditch that possibly encircled the entire site, and an earthen wall, where more than 100 burials, mostly secondary, were uncovered. The foundations of 24 round, rectangular, and pile-dwellings (marked by numerous post-holes), as well as two houses erected on earth platforms, were documented (Hunan Provincial Institute of Cultural Relics and Archaeology 2006). The faunal assemblage includes wild cattle, various deer species, wild boar, rats, and birds. Fish and turtles were retrieved from local fresh water bodies.

Both sites are rich in pottery remains with a variety of vessel types as well as clay stands that served as supports for the pots while cooking above fires. Stone tools are similar, including a few polished axes and some adzes, choppers, and bone and shell tools. The material culture from both sites serves as the basis for the definition of the Pengtoushan Culture.

Numerous charred rice grains from Bashidang were dismissed by one researcher as wild (Fuller *et al.* 2007), whereas a recent study demonstrates (H. Gu, personal communication 2008) that the measurements of whole grains, and types and size of embryos, indicate that by *c.* 8,000 BP a high percentage of the collection of charred seeds were already within the range of domesticated rice.

The Lower Yangtze River region is currently the main provider of archaeobotanical information. For example, at Shangshan (Zhejiang), a 60 cm deep site with evidence for multi-period occupations, dated pottery fragments (*c.* 9,950–8,900 BP) attributed to the earliest layer suggest that the plant matter embedded in the ceramics include some rice chaffs after hulling, rice husks, and phytoliths, that indicate not just the collection of wild rice but perhaps an initial phase of rice cultivation (Zhejiang Provincial Institute of Cultural Relics and Archaeology 2005, Jiang and Liu 2006, Zheng *et al.* 2007).

Xiaohuangshan, known from preliminary reports, with controversial dating, is about 5 ha in size and produced a large number of houses, many pile-dwellings, graves, pits, and a rich pottery assemblage. Unfortunately its plant and animal remains are not yet reported.

It is Kuahuqiao (*c.* 8000/7700 to 7500 BP; Figure 3.3) that occupies a major position in reconstructing the sequence from cultivation of wild rice to the increasing frequencies of the domesticated variety. The site is about 3 ha in size and had exceptional preservation. The most striking was a major portion of a canoe, a bow, and various timbers and planks, some covered pits, and a rich collection of plants and animal bones (Zhejiang Provincial Institute of Cultural Relics and Archaeology, 2005).

The study of phytoliths as well as the carbonized rice grains and rachillae indicated that about 42% are of the *Oryza japonica* cultigen, signified by short rachillae, while the rest exhibited the features of the wild type (Zheng *et al.* 2004, 2007). The interpretation that the small size of the seeds indicate their immature state (Fuller *et al.* 2007) was rejected, but others have agreed (e.g., Zhao submitted). Another angle for consideration is the proposition from an independent environmental investigation that the cultivation of wild rice took place in the wetlands around the site, controlled by embankments that formed a sort of simple paddy-like fields (Zong *et al.* 2007).

The conclusions concerning the farming activities in Kuahuqiao resemble the results obtained by Tanno and Willcox (2006) concerning the increasing frequencies of domesticated cereal ears in the northern Levantine sites by *c.* 10,500 BP. Cultivation as a practice by farmers during a millennium or millennium and a half, although not necessarily in one long-existing site, allowed the cultigens to take over the fields. One can view this process as the results of several trials, in various localities, by the same general population (Weiss *et al.* 2006).

The faunal assemblages of Kuahuqiao, retrieved from the two main layers, demonstrate an interesting shift. The assemblage of the lower layer consisted mainly of pig, deer, elk, water buffalo, and dogs; the upper layer shows an increase in deer frequencies at the expense of the pigs (Yuan *et al.* 2008). On the basis of morphometric traits the pigs have been identified as domesticated, yet wild mammals (mainly deer species), abundant in the natural habitats of this alluvial and hilly region, continued to dominate the faunal assemblages in Kuahuqiao and several sites until 4,000 BP (Flad *et al.* 2007, Yuan *et al.* 2008).

Kuahuqiao marks, in the schematic subdivision, the onset of Middle Neolithic, well known from the earlier excavations of the waterlogged Hemudu site (7,000–6,500 BP) and recently the ongoing project in Tianluoshan. Both sites, with numerous rectangular pile-dwellings, produced sufficient evidence that cultivating rice was one of the many activities in these villages. A recent study (Fuller *et al.* 2009) demonstrates the gradual shift in the fields from wild rice to increasing domesticated forms from 27.4% to 38.8%, accompanied by increasing frequencies of arable weeds. The change took place from *c.* 6,900 to *c.* 6,550 BP, thus during three and half centuries.

In all these villages gathering, hunting, and fishing (a rich resource in the Yangtze River) continued to produce the main components of the local diet. Collecting edible aquatic plants such as caltrops, water chestnuts, water dropwort, water spinach, and, in drier areas, fruits including jujube and acorns, as well as bottle gourds, that could have been used as containers, were recorded. Numerous pits with acorns testify to the importance of this source of food. Hence, referring to these villages in the past as “affluent foragers” (e.g., Chang 1981) misses the point that they were also cultivators, and, as it seems today, without systematic annual cultivation the plants could have never become domesticated. A detailed discussion by Crawford (2008) of plant remains in Jomon settlements makes it clear that cultivation of particular plant species took place in village

contexts long before rice cultivation was introduced from Korea *c.* 2,800 BP. Hence, whether we define the sites as the locations for “low level food production” or not, cultivation means that the inhabitants were farmers, whether part-time or full-time, and the term “agriculture” can be attributed to their economy.

In sum, the excavations of open-air sites in the Yangtze River basin and caves in the hilly areas further southwest, produced a more or less continual sequence from foraging to farming. Among the main characteristics is the production of pottery during the Upper Palaeolithic, from *c.* 18 ka BP, that possibly reflects a new way of using plant foods for making drinks and only later, when the quality of the pots improved, for cooking. The stone artifacts demonstrate a high degree of conservatism, with the appearance of polished axes and well-shaped adzes from 11/10 ka BP. Bone and antler tools (including harpoons) as well as shell tools interpreted as reaping knives, are integral parts of the late Upper Paleolithic tool kits. It is as yet unknown when systematic cultivation of cereals began but by *c.* 8,000 BP it seems that domesticated forms were increasingly present in the fields. The first small paddies uncovered in Chengtoushan (Hunan; *c.* 5,600 BP; Nasu *et al.* 2007) indicate that by that time, instead of using natural wetlands as suggested by the investigations near Kuahuqiao, cultivation was practiced in an anthropogenically shaped landscape. Hunting, fishing, and gathering in rich aquatic and forest environments produced animal tissues during most of the Early and Middle Holocene. Migratory birds often reflect winter occupations and rare indications for the presence of commensals support the contention of all-year round sedentism in the Yangtze Neolithic villages. Communication by river craft, including canoes or bamboo rafts, ensured the transmission of information over long distances and the arrival of rice in the Yellow River basin at an early age as indicated above.

8 Concluding remarks

When viewed from the angle of a *longue durée*, subsistence strategies adopted by foragers during the Terminal Pleistocene and early Holocene in western and eastern Asia have much in common. In a land “full of people” the winning option was to stay put, defend and exploit local resources, and intensify returns by cultivation of well-known plants. This is best achieved in the natural habitat of the progenitors. None of the “foragers in transition” ever abandoned gathering, hunting, and trapping of wild mammals, reptiles, and birds, as demonstrated by the archaeozoological and archaeobotanical records from both ends of Asia. Part-time cultivation with continued gathering and hunting can be labeled as we wish. We may label the people as “incipient farmers” or “affluent foragers” who practiced “low level food production”, but we should be aware of their entire suite of subsistence strategies. In most but not all cases in the Levant and North and South China, “incipient cultivation” led to rapid increases in

population and the development of full-fledged farming and herding economies. Each region, however, had a different evolutionary pace.

Over the first four millennia of the Holocene (*c.* 11,700/500 through *c.* 8,200/8,000 BP), the process of annual cultivation of cereals in the Levant ended in the domestication of several species as well as a suite of other plants (legumes, flax, etc.). Corralling and domestication of selected animals in the northern Levant (goat and sheep, cattle, and pig) was a significant addition to the foundations of the agricultural economy of later periods. In China, the main domesticated animals were pigs and dogs as well as the chicken. Further species were added later.

After *c.* 10,500 through 8,200 BP, farming communities rapidly evolved in western and eastern Asia and populations increased – a phenomenon labeled the “Neolithic Demographic Transition”. This rapid growth was not limited to Asia alone but occurred after the establishment of the so-called “Neolithic” economy in other regions as amply described and analyzed by Bocquet-Appel and others (e.g., Bocquet-Appel and Bar-Yosef 2008 and papers therein). The dating of this demographic shift across various regions reflects the different paces at which the transition to full farming-based subsistence took place. The wide spread of the Neolithic Demographic Transition makes it clear that this economy was the winning strategy, and its consequences are well known historically. However, it should be stressed that it does not mean that every human group or ethno-linguistic entity joined this endeavor. Suitable farming lands were colonized by the advancing agricultural societies who limited the territories of hunter-gatherers. The study of the nature of interactions between farmers and foragers is an increasingly popular topic in current literature and is critical for understanding not only the origins and spread of agriculture, but also the later social and economic developments.

In sum, in considering the current archaeological knowledge from China as compared to the Levant, we may conclude that the loess plateau and river valleys in the North, similarly to historic times, were more often prone to droughts than South China or the Mediterranean vegetational belt. The latter regions almost always enjoyed rainy winters or subtropical and tropical conditions due to the westerlies or the monsoons. It should be stressed that all three regions, as reflected in the speleothems and pollen cores, and in spite of the major size discrepancies among them, demonstrate a considerable amount of environmental variability, and should be treated as major “paleoecological mosaics”.

If the arguments brought forward in this chapter, in the footsteps of several scholars, are correct, then we should expect to find communities cultivating wild millet in North China earlier than the earliest cultivators of wild rice in the South, similarly to what we expect in the Levant. The differences in site size between North and South China, where the much larger ones were in the former, may support this contention. In the three regions it took a long time between the first emergence of the domesticated varieties and their ensuing dominance in the fields, as is indicated by various studies (e.g., Weiss *et al.* 2006, Lee *et al.* 2007, Liu *et al.* 2007, Willcox *et al.* 2008, 2009, Fuller *et al.* 2009).

Attributing incipient cultivation as a chosen food-procuring strategy under worsening environmental conditions is among the several behavioral options that hunter-gatherers had while trying to minimize risks to their survival and create economic buffer conditions. Their choice to start cultivation as part of their planned annual food acquisition strategies was not always successful. Other options were viable as well, such as to move to other peoples' territories, which in China could have happened along waterways, but this would have also meant facing inter-group conflicts. Increasing sedentism in preferred ecological niches and minimizing mobility had its advantages but the risks of "scalar stress" leading to social splitting were at first an unconscious result. Apparently, in all three regions small-scale farming was added to large-scale gathering, hunting, trapping, and fishing. But those who insisted on cultivating cereals were eventually the long-term winners. Cereal cultivators gained by enabling the fertility rate of females to increase and by providing weaning food for newborns, thus resulting in population growth that facilitated territorial control and expansion.

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4 Pre-Domestic Cultivation during the Late Pleistocene and Early Holocene in the Northern Levant

George Willcox

Pre-domestic cultivation, or sowing and harvesting, of morphologically wild plants was an inevitable step in the adoption of cultivation which led to the development of agriculture in the ancient Near East. The overall transition from gatherers to established farmers with domestic crops probably spanned three millennia (Tanno and Willcox 2006, Fuller 2007). At a number of archaeological sites which date from 13,000 to 10,000 BP, remains of wild progenitors have been interpreted to be the result of cultivation rather than of gathering. Van Zeist and Bakker-Heeres (1986) and later Colledge (1998, 2001) suggested the possibility of pre-domestic cultivation for twelfth millennium levels at Mureybet. Van Zeist also used similar arguments for later levels at Cayönü (van Zeist and de Roller 1994). Hillman *et al.* (2001) argued for cultivation at the Epipalaeolithic site of Abu Hureyra, dated to about 13,000 years ago. In the southern Levant, Kislev (1997) argued for pre-domestic cultivation at Netiv Hagdud, dated to about 11,300 years ago, and Edwards *et al.* (2004) argued the same for Zahrat adh-Dhra. While it is fair to say that there is a consensus of opinion that pre-domestic cultivation predates morphological domestication by a millennium or more (Tanno and Willcox 2006, Fuller 2007, Brown *et al.* 2009), reliable data to confirm this hypothesis are hard to come by.

Archaeobotanical analyses of charred remains from recent excavations at Jerf el Ahmar in northern Syria have allowed us to identify pre-domestic cultivation with more certainty than before. Jerf el Ahmar is part of a complex of sites, dated to between *c.* 11,500 and *c.* 10,300 BP, (Figure 4.1) characterized by communal buildings, importation of precious materials, and sophisticated symbolic representations. Of the tens of thousands of cereal remains identified from these sites, all were morphologically wild (Figure 4.2). There was no evidence of morphological cereal domestication identified from nonshattering ears or nondehiscent pods in the case of legumes. As we shall see, in-depth studies of the charred material (Willcox *et al.* 2008, 2009) have produced evidence pointing to a long period of pre-domestic cultivation lasting from 11,500 to 10,300 BP. Indeed it is possible that small-scale cereal cultivation started some 13,000 years ago at Abu Hureyra (Hillman *et al.* 2001). But at this site cereal grains were far less frequent

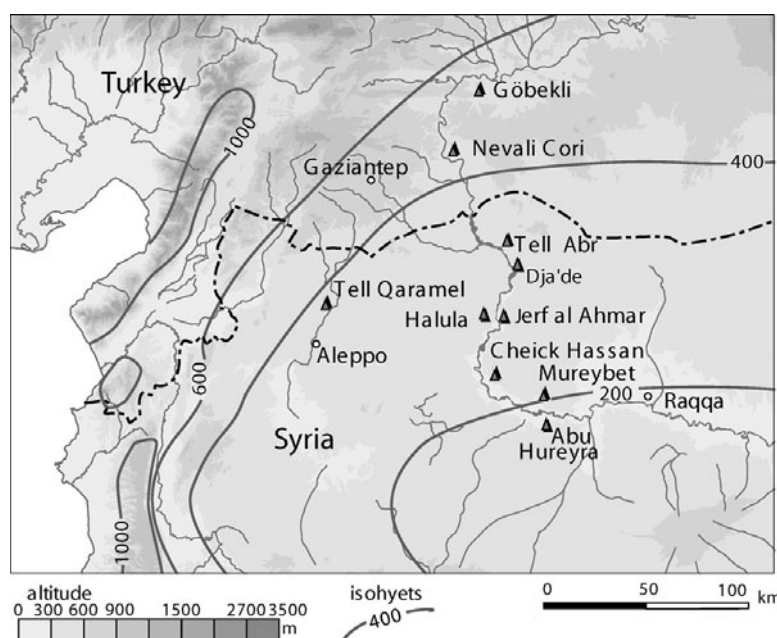


Figure 4.1. Position of the major sites mentioned in the text. Isohyets are given to show the rainfall gradient. Hallan Çemi (Table 4.1) is situated off the map to the northeast.

than seeds from nonfounder plants gathered from the flood plain, which continued to play a major role until the climatic amelioration of the early Holocene (starting c. 11,500 BP) when cereals and pulses became the dominant staples (Willcox *et al.* 2009).

Evidence presented here for the Euphrates sites demonstrates a protracted period of pre-domestic cultivation where the importance of the cereal economy is manifest in archaeological findings other than charred remains. Looking farther afield beyond the northern Levant, researchers are beginning to see a similarly complex and drawn-out process with a prolonged period of cultivation prior to domestication, for example in the southern Levant (Weiss *et al.* 2006, Feldman and Kislev 2007) and also in the Far East (Fuller 2007). Recent DNA work on einkorn, emmer, and barley are also showing a more complex picture (Kilian *et al.* 2006, 2007, Luo *et al.* 2007) compared with early studies (Heun *et al.* 1997).

1 The archaeological sites

In this section I give a brief description of the major sites mentioned in the text. For more detail the reader will need to refer to the archaeological reports. For site location and rainfall patterns the reader is referred to the map in Figure 4.1. Dating of the sites was based on a large number of ^{14}C dates. All dates are given as

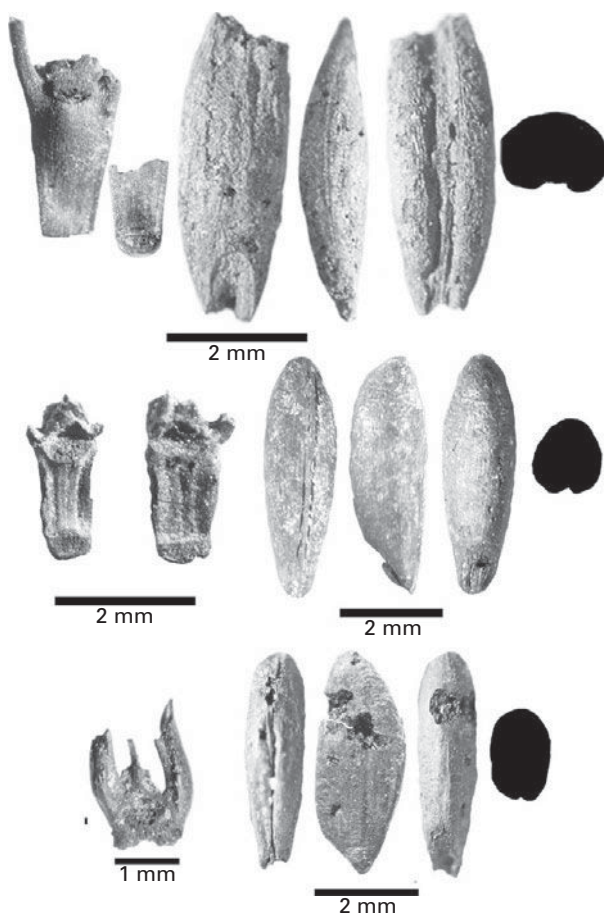


Figure 4.2. Charred wild cereal spikelet bases (left) and grains (right). Top, *Hordeum spontaneum* (wild barley) from Jerf el Ahmar. Middle, *Secale* sp. (rye) from Jerf el Ahmar. Bottom, *Triticum boeoticum* (single-grain einkorn) from Tell Qaramel. Note the basal abscission scar seen in the barley (top row, second from the left) and for rye the lower end of the rye spikelet bases (second row, first and second from left) is more reliable than the upper scar for distinguishing between wild and domestic.

calibrated years before present (BP). Date ranges for each site are given in the two upper lines in [Table 4.1](#). The two earliest sites date to the end of the Pleistocene. Abu Hureyra 1 is late Natufian (13,250 to 12,750 BP), with occupation levels that date to the end of the Allerød and the beginning of the Younger Dryas. Not far away at Mureybet, the earliest levels (Mureybet 1) date to the final Natufian (12,500 to 12,000 BP) and coincide with the second half of the Younger Dryas (Ibañez 2008). The succeeding levels of Mureybet 2 are Khiamian (12,000 to 11,500 BP), and farther west at the site of Tell Qaramel the early levels date to the same period. The sites which concern us here, often termed PPNA, make up a complex of five sites which are situated at regular intervals along the left bank of the Euphrates. They were occupied at the beginning of the Holocene between

Table 4.1. Absolute counts of edible taxa identified from a selection of sites in the northern Levant where there are no signs of morphological domestication

Nonedible plants were excluded. The so-called founder crops (cereals and pulses) increase at the expense of nonfounder plants gathered from the flood plain during the early Holocene. Date ranges for the sites are based on calibrated ¹⁴C dates, which are given in the top two rows. Low sample numbers from Tell ‘Abr and Mureybet make these data less reliable.

	Abu Hureyra 1	Mureybet 1	Mureybet 2	Qaramel	Hallan Çemi	Tell ‘Abr	Mureybet 3	Jerf el Ahmar 1	Jerf el Ahmar 2	Dja’de
from calBP	13,250	12,500	12,000	12,000	11,500	11,500	11,500	11,500	11,200	11,000
to calBP	12,750	12,000	11,500	11,500	11,200	11,200	11,200	11,200	11,000	10,300
<i>Secale/Triticum</i> grain	888	12	8	1,170	19	2,999	2,000	1,382	1,055	1,120
<i>Triticum</i> spikelet base	0	0	0	292	0	0	0	0	5	16
<i>Secale</i> sp. spikelet base	0	0	p	0	0	0	p	121	22	16
<i>Hordeum spontaneum</i> grain	0	3	2	217	124	190	164	2,353	6,474	3,763
<i>H. spontaneum</i> spikelet base	0	0	0	0	0	?	6	1,546	1,746	153
<i>T. b. aegilopoides</i> grain	0	0	0	1,108	0	90	1	18	49	302
<i>T. dicoccoides</i>	0	0	0	4	0	0	0	0	0	192
<i>Lens</i> sp.	48	1	6	1,113	11	230	28	452	1,147	5,850
<i>Pisum/Vicia/Lathyrus</i>	48	1	6	682	748	37	13	146	237	1,952
<i>Cicer</i>	0	0	0	0	0	0	0	0	0	3
<i>Vicia faba</i>	0	0	0	0	0	0	0	0	0	2
<i>Vicia erilia</i>	3	0	0	11	29	0	4	10	46	34
<i>Stipa</i>	1,573	0	0	526	76	0	0	2	51	272
Panicoid grasses	342	35	35	1	0	0	24	19	1	0
Cyperaceae	4,776	51	59	242	4,415	0	22	15	14	32
<i>Rumex/Polygonum</i>	4,848	312	1,037	11	3,748	0	351	359	126	37
<i>Ficus carica</i>	0	0	0	4	0	0	3	1	10	42
<i>Amygdalus</i> spp.	0	0	0	2,214	179	0	0	760	666	2
<i>Pistacia</i> sp. fragments	357	8	10	1,705	120	0	12	1,302	1,274	911
Rodent droppings	0	0	0	49	0	0	0	8	39	221
Totals of edible plants	12,883	423	1,163	9,300	9,469	3,546	2,628	8,486	12,923	14,920
Volume of sediment (l)	7,925	?	?	1,772	19,393	452	?	6,210	5,904	6,122
Number of samples	21	11	22	108	175	30	27	154	81	229
	Late Natufian	Late Natufian	Khiamian	Khiamian	PPNA	PPNA	PPNA	PPNA	PPNA	Early PPNB

Sources: Data for Abu Hureyra were provided by Sue Colledge, research assistant at the Institute of Archaeology, London. Data for Mureybet are from van Zeist and Bakker-Heeres (1986); for Jerf el Ahmar, Tell ‘Abr, Dja’de, and Tell Qaramel, data are from Willcox *et al.* (2008). Data for Hallan Çemi provided by Manon Savard, Université du Québec à Rimouski.

11,500 and *c.* 10,300 years ago during a period of climatic amelioration (Willcox *et al.* 2009). These include Mureybet 3, Cheik Hassan, Jerf el Ahmar, Tell ‘Abr and the recently discovered early levels at Dja’dé, which also contains early PPNB levels. These sites are very similar in their architecture, symbolism, and chipped stone, suggesting cultural unity (Stordeur 2000, Stordeur *et al.* 2000). Further north in southeast Turkey, sites such as Demirköy, Göbekli (Schmidt 2006), and Hallan Çemi (Peasnell *et al.* 1998) also possess strong parallels (Helmer *et al.* 2004), but the plant economy at these more northern sites may have been different.

At Abu Hureyra, excavators found small shallow pits, which they interpreted as rudimentary dwellings (Moore *et al.* 2000). At Tell Qaramel (Mazurowski 2004), situated on the river Quwayq about 25 km north of Aleppo, much bigger round houses were found, constructed in stone and earth with well-defined hearths. In one house a large number of bucrania were found. Artifacts include Khiamian arrowheads and a rich ground-stone industry with chlorite bowls, shaft straighteners, querns, pounders and “batons polis”. Similar objects also occur on PPNA sites in the area (Stordeur 2000, Stordeur *et al.* 2000). At Jerf el Ahmar the houses from the earliest levels are similar to those excavated at Tell Qaramel. Later levels have produced rectangular houses and large, sunken, round communal buildings, which were also found at Mureybet 3 and Tell ‘Abr (Yartah 2004, 2005). Dja’dé (Coqueugniot 2000) is chronologically the youngest site, dated to 11,000 to 10,300 BP. It has the oldest known geometric wall paintings in the Near East, which decorated a large, possibly communal building.

2 Large-scale use of cereals at Jerf el Ahmar

How important were cereals in the subsistence economy of PPNA sites? At the sites of Hallan Çemi and Demirköy in southeast Turkey, cereals are rare compared with other grains and so probably represented a minor component of the diet (the same was probably true for Natufian Abu Hureyra; see Table 4.1). In contrast, at Jerf el Ahmar 14,771 remains of charred wild barley, wild rye, and wild einkorn were recovered from occupation layers, suggesting that these cereals were a major component of the diet (see Table 4.1). Frequencies alone give a limited picture of the role of different food plants; thus my colleague Danielle Stordeur and I investigated the archaeological evidence for the role of cereals (Stordeur and Willcox 2009). We found that, like the charred grains, artifacts associated with processing were found throughout the site, particularly stone saddle querns, which were used to grind grain (Willcox 2002b). The arrangement of the querns is very instructive. Many were found in situ inside the buildings, frequently occurring three to a room, suggesting that grinding was being practiced in an organised manner with three querns working simultaneously in a single architectural and social unit. Figure 4.3 shows a room with a row of three quern bases which date to the later stages of the site, *c.* 11,000 BP. The querns were immobilised and made stable by being set into solid bases. The layout of the



Figure 4.3. Settings for three saddle querns in a room excavated at Jerf el Ahmar. Other rooms contained similar arrangements of querns, suggesting that cereal processing was being practiced on a large scale. Photo with permission from D. Stordeur.

querns suggests that cereals played an essential role in the everyday economy of the site and that cereal processing was probably intertwined with the social structure of village life (Stordeur and Willcox 2009).

Prior to the grinding of grains, dehusking was carried out to separate the edible grain from inedible chaff consisting of glumes and spikelet bases. The latter were found in vast quantities in the form of impressions in building earth at Jerf el Ahmar, Tell ‘Abr, and Mureybet. The building earth was made of a mixture of fine sediment to which cereal chaff was added as a tempering medium to reduce shrinkage and increase strength (Willcox and Fornite 1999). This technique is still used today in many parts of the world, including northern Syria. When the buildings burned at Jerf el Ahmar (a frequent occurrence), the earth was baked and hardened, leaving perfect impressions of the chaff, consisting of awns, glumes, lemmas, and spikelet bases, which were finely fragmented (see Figure 4.4), suggesting that dehusking was carried out by pounding, perhaps in a wooden pestle with a mortar. Examination of large quantities of building earth showed that chaff was systematically used as a tempering medium. Buildings at Jerf el Ahmar were constructed from local chalk, covered with 5–10 cm of earth. Similarly, the roofs were constructed with wooden beams between which were laid twigs, straw, or reeds, which were then covered with chaff-tempered building earth. Chaff must have been available in massive quantities given the size of the buildings at Jerf el Ahmar and the fact that they were regularly maintained, destroyed, and rebuilt. The quantity is surprising if we take into account that the dehusking of hulled cereals, particularly barley, produces a low proportion of chaff to grain. Quantifying the volumes would be difficult, but common sense suggests that we are dealing with considerable volumes, which would have to be stored.

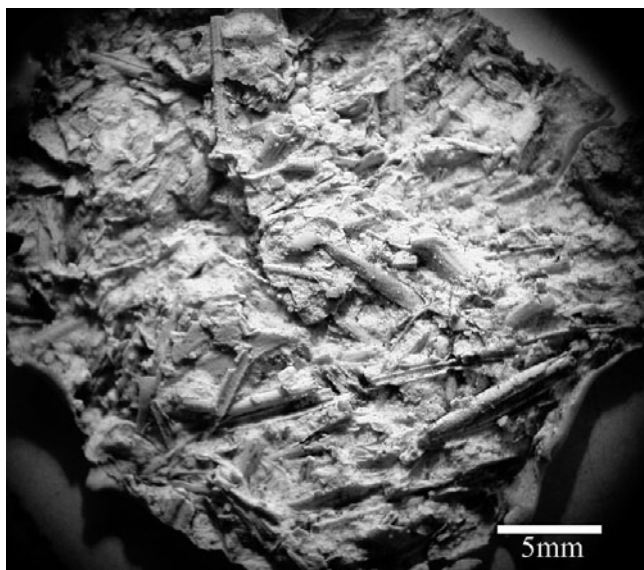


Figure 4.4. Photograph of a silicone cast of a fractured fragment of building earth from Jerf el Ahmar showing elements of cereal chaff. The chaff obtained from dehusking, mainly barley and rye, was used systematically as a tempering material in the building earth. This demonstrates that large quantities of chaff would have been available and that they would have to have been stored, ready for use when building work was carried out.

After the harvest and initial threshing to remove the straw, whole spikelets were probably stored prior to dehusking. Storage occurred in communal buildings at Tell ‘Abr and possibly at Mureybet, where large quantities of pure charred cereal grain were found. Small cells (silos) located in the communal buildings at Jerf el Ahmar were used for storage (Stordeur *et al.* 2000). Indirect evidence for storage at Jerf el Ahmar comes from charred rodent droppings, many of which correspond in size to those of the domestic house mouse. Indeed, six archaeozoological finds of domestic mice (*Mus musculus domesticus*) were identified at Dja’de and one at Jerf el Ahmar (Cucchi *et al.* 2005). These mice most probably fed on stored grain. In total 47 charred droppings were found at Jerf el Ahmar and 221 at Dja’de (Table 4.1). Other early village sites where domestic house mice have been found include Hyonim B and Netiv Higdud in the southern Levant, and Mureybet and Cafer Höyük in the north. Domestic mice were introduced to Cyprus by about 10,500 BP (Cucchi *et al.* 2005) and this may imply that important quantities of cereal were regularly imported.

Further evidence for intensive cereal use comes from finds of flint harvesting blades. They were identified by their characteristic gloss, caused by the build-up of a film of plant silica on the cutting edge of the tool (Anderson 1999). At a few sites these blades have been found hafted with bitumen in stone, bone, or wooden (charred) sickle handles. None were found at Jerf el Ahmar. These tools can be used for harvesting wild stands or cultivated fields. At Jerf el Ahmar and

contemporary sites on the Euphrates there is an increase in both size and quantity of these tools compared with earlier sites (F. Abbès, pers. commun.). This coincides with an increased reliance on cultivation.

3 Pre-domestic cultivation at Jerf el Ahmar

Five lines of evidence suggest that pre-domestic cultivation was practiced at Jerf el Ahmar during the early Holocene. Arguments in favor of cultivation of wild cereals and pulses were described in detail in an article published recently (Willcox *et al.* 2008). The following is a summary.

3.1 The decline of gathering

At Jerf el Ahmar a gradual reduction in gathering can be seen between lower and upper levels by the diminished frequencies of small-seeded grasses such as *Stipa*, panicoid types, and also other small-seeded grains such as Cyperaceae and *Polygonum/Rumex* (see Table 4.1 and Willcox *et al.* 2008). The decline in the gathering of these seeds was compensated for by an increase in the use of founder crops, notably barley, emmer, einkorn, lentil, and pea, which were probably cultivated. It appears that these changes in plant use represent an increasing reliance on cultivation.

3.2 The introduction of crops

In order to observe this we need to compare the presence of cereals and pulses across a wide chronological sequence in the Euphrates region of northern Syria. Thus we see that rye and two-grained einkorn were the only cereals present at late Pleistocene Abu Hureyra. At later sites such as Jerf el Ahmar, first barley, then single-grained einkorn and emmer were introduced. Climatic amelioration at the beginning of the Holocene may have opened the way for a wider choice of crops than those occurring locally. Pulses were also introduced; this can be seen at Dja'de, the most recent site where *Vicia faba* and *Cicer* were introduced from their natural habitats, which were probably located at a considerable distance.

3.3 Weeds of cultivation

Weeds of cultivation are plants that thrive when the soil is disturbed by cultivation. They have been evolving since the Neolithic and increasing in numbers as agriculture spread into new habitats. We examined (Willcox *et al.* 2008) the possibility of weeds taxa being present at Jerf el Ahmar as indicators of cultivation. Fifty-four taxa of wild and/or weed taxa were identified from charred seeds. Some, such as *Androsace maxima*, *Hyoscyamus*, *Peganum hamala*, and *Tribulus terrestris* were ruderals probably growing near the habitations. Others, for

example the small legumes, *Alyssum/Lepidium*, and wild grasses, could have been used as food plants before the advent of cultivation so they cannot be used as indicators of cultivation. Fifteen taxa that have no known use and are typically weeds of cultivation in modern fields and on Bronze Age sites, where the question of cultivation is not in question, were interpreted as weeds of cultivation. This number is small presumably because at this stage few species had had the time to come into contact with cultivation. The comparison of potential weed taxa from sites sampled in a similar way is revealing. Significantly, there is an increase in the number of taxa as cultivation becomes more of a possibility. Of the fifteen taxa from Jerf el Ahmar, only one occurs at Ohalo II (Kislev *et al.* 1992), eight at Abu Hureyra, and twelve at Tell Qaramel (Table 4.2). Some taxa may have occurred at low frequencies in wild cereal stands; as cultivation gained ground more species became incorporated into the new habitat, which is why the number and quantity of weed taxa increase.

3.4 Increase in grain size

An increase in grain size is often cited as a sign of domestication (Hillman *et al.* 2001). A study of barley grain size at Jerf el Ahmar and Dja'de demonstrated that there is a small increase in thickness and breadth between the lower and upper levels but that in the same geographical area there is no further increase for several millennia (Willcox 2004). This size increase could be due to phenotypic changes resulting from improved growing conditions or selection resulting from long-term cultivation. A third possibility is the introduction of a plump-grained population from elsewhere. It is improbable that genetic selection for plump grains would precede selection for nonshattering ears, because the former is complex and involves multiple genes compared with the latter (loss of dispersal) which involves one or two genes. For this reason it is probable that this increase represents a cultivated population where a higher proportion of grains reached full development compared with a wild population, where growing conditions would be variable and include marginal habitats, leading to a higher proportion of poorly formed grains. The other relevant species, einkorn, is problematic because of the difficulty of separating these grains from rye and because einkorn populations consist of two-grained and single-grained varieties, which are different in size but their proportions change. To conclude, it is possible that if cultivators chose the best soils for cultivation then this could result in an increase in grain size compared with populations from the wild.

3.5 The location of sites beyond wild cereal habitats

At most late Pleistocene/early Holocene sites in the Near East, the cereals identified correspond to those which one would expect to be growing locally and occur in the present-day vegetation. An exception is to be found at sites on the Euphrates in northern Syria, which today is an area too arid for wild einkorn

Table 4.2. Weeds of cultivation present at different sites in the Near East

The number of the taxa present at these sites increases with time. These sites were all extensively sampled so the increase may well result from cultivation, which became more intense. P, present; A, absent.

Taxon	Jerf	Qaramel	Hallan Çemi	Abu Hureyra	Ohalo II
<i>Centaurea</i>	P	A	P	A	A
<i>Fumaria</i>	P	A	P	A	A
<i>Trigonella</i>	P	P	A	A	A
<i>Coronilla</i>	P	P	A	A	A
<i>Onobrychis</i>	P	A	A	P	A
<i>Erodium</i>	P	A	A	P	P
<i>Thymelaea</i>	P	P	P	A	A
<i>Adonis</i>	P	P	P	A	A
<i>Alyssum/Lepidium</i>	P	A	P	P	A
<i>Glaucium</i>	P	P	A	P	A
<i>Heliotropium</i>	P	P	P	P	A
<i>Silene/Gypsophila</i>	P	P	P	P	A
<i>Trifoliae</i>	P	P	P	P	A
<i>Bellevalia</i>	P	P	P	P	A
<i>Galium</i>	P	P	P	A	P

and wild rye. The most southerly sites are almost 200 km south of present-day wild rye habitats and between 100 and 150 km south of wild two-grained einkorn habitats. With the cooler climatic conditions of the late Pleistocene these cereals may have extended farther south. How far south is difficult to estimate. Willcox (2005) pointed out that within today's natural distribution, rye does not occur on poor soil that develops on chalk bedrock, so despite cooler climatic conditions it is improbable that wild rye could have grown near the sites of Jerf el Ahmar and Abu Hureyra where these poor soils are found. However, Hillman *et al.* (2001) suggested that rye may have grown farther south during the Allerød, but that with the onset of the harsh climatic conditions of the Younger Dryas it would have retreated. They argued that the continued use of rye during the Younger Dryas at Abu Hureyra 1 implies that it was cultivated. Rye was also found at Mureybet 1 in levels corresponding to the Younger Dryas. At both these sites rye and einkorn are found at low frequencies compared with grains gathered from the flood plain.

Given that these sites are far from wild stands, several scholars discussed the possibility of transportation of grain. The distance between wild stands and villages could have increased as climate conditions forced wild stands to retreat, creating the need to import from farther and farther afield. Theoretically, imported grain from wild stands may have been used initially for consumption; a second step might have been the annual importation of grain from wild stands for sowing near the sites where the harvest from cultivation would be for consumption. This practice could have occurred for a prolonged period. Then a third step may have been sowing the grain harvested from cultivation. This would only

have happened if a surplus could be regularly relied upon from cultivation, which would eventually provide a local, secure, and dependable supply of grain. But this leads us to ask whether it was possible to cultivate wild rye and two-grained einkorn in areas where these plants would not have grown in the wild. The answer is yes, because under cultivation, fields would have been chosen in edaphically favorable locations, creating a microhabitat where competition from other plants had been removed (Valkoun *et al.* 1998, Willcox 2005). But there came a point when climate conditions became too extreme, which is why rye declines and barley increases at Jerf el Ahmar, the latter being much better adapted to the climate and soils of the Euphrates basin in northern Syria.

In summary, the arguments in favor of cultivation as opposed to gathering of wild cereals at Jerf el Ahmar only stand up to scrutiny when taken together. These arguments are reinforced by the evidence for large-scale cereal use outlined above; this does not exclude the possibility that gathering continued as a supplement. Given that five other sites on Euphrates, Tell 'Abr, Dja'de, Mureybet, and Cheik Hassan, have a similar material culture (Stordeur 2000) and are close geographically, it is possible that the inhabitants at these sites also cultivated cereals and pulses. But we should be careful not to extend our assumptions too far because at contemporary sites situated farther east and north such as Göbekli Tepe, Hallan Çemi, Demirköy, Nemrik, Qermez Dere, and M'lefaat (Neef 2003, Savard *et al.* 2006) there is less evidence and these authors interpret these sites as being inhabited by gatherers.

4 When did domestication appear?

In the Euphrates valley of northern Syria, reliable signs of morphological domestication, indicated by the partial loss of the dispersal mechanism in emmer and barley, are found in the earliest levels at the sites of Halula and Abu Hureyra 2, dated to *c.* 10,000 BP. These are full-scale farming sites, which have domestic animals and cover a surface area at least ten times larger than the PPNA sites. Elsewhere the same tell-tale abscission scars left on spikelet bases were found at the sites of Nevali Çori, Cayönü, and Cafer Höyük dated to *c.* 10,500 years ago. The later date for domestication on the Euphrates in northern Syria may be due to a gap in the archaeological record. At these early domestication sites, wild types persist alongside the domestic types (van Zeist and de Roller 1994, de Moulin 1997, Pasternak 1998, Tanno and Willcox 2006).

5 Why was morphological domestication slow to become established?

Theoretically, less than 200 years of cultivation could have selected for a domestic population (Hillman and Davies 1990). Yet there is no evidence for plant domestication as seen in the loss of dispersal mechanisms for either

cereals or pulses at the Euphrates sites, despite prolonged cultivation. Cereals remained wild at least until 10,300 years ago, as seen at Dja'de, and this, at least 1,000 years after the first signs of cultivation at Jerf el Ahmar. Why, then, did domestication not appear earlier? One reason is that seed stock may have been regularly replenished from wild stands to counter poor harvests (droughts, disease, etc.), which may have been a frequent occurrence in the arid middle Euphrates. Another reason is that harvests may have occurred early in the season before the ears shattered, which would mean that the probability of selection for the rare mutants that had lost their dispersal mechanism would be extremely slim, and nonshattering ears would have had little advantage. We know that ears which shatter compete well with nonshattering ears in cultivated fields because wild einkorn and barley are common weeds of cereal fields in the Near East today. Studies on a wider geographical scale and for a variety of cereals indicate that morphological domestication was slow to be established and mixed populations of wild and domestic cereals persisted side by side for long periods (Fuller 2007, Tanno and Willcox 2006). This continued admixture suggests that during the early Neolithic, nonshattering and shattering forms were inseparable and so similar that Neolithic farmers treated them both as part of the crop.

Finally, on theoretical grounds, creating a population from a single mutant plant by conscious or unconscious selection would have the disadvantage of reducing genetic diversity, which was necessary to create crops with good yield stability (Abbo *et al.* 2010). Conscious selection is highly improbable for barley and wheat crops because domestic traits are not readily visible to the naked eye. In addition a single line would not have been viable under cultivation given the heterogeneous and irregular climatic and edaphic conditions, not to mention resistance to pathogens. This leads us to the conclusion that in order for healthy crops to develop they would need to have a variety of landraces consisting of several genotypes, as can be seen in pre-industrial crops.

6 Climate change and the adoption of cultivation

There are no palaeoclimate records or pollen spectra for the middle Euphrates region in northern Syria. For palaeoclimate reconstruction we have to rely on (1) information on past vegetation from the archaeobotanical record, (2) pollen cores from lake sediments, which occur far from our area, and finally (3) ice core data, which provide high-resolution information on global climate change.

How did climate change affect the availability of food plants in northern Syria? The early levels at Abu Hureyra 1 coincide with the Allerød. Temperatures were probably lower than at present. The pollen record indicates that forest vegetation was expanding in low-lying areas near the Mediterranean coast during this period and this may have been the case in northern Syria

because charcoal and seed analyses from Abu Hureyra indicate a forest–steppe vegetation consisting of *Pistacia atlantica* trees, grasses, and occasional oaks (Hillman 2000, Roitel and Willcox 2000, Willcox 2002a). These taxa occur today in vegetation zones found at higher altitudes. The use of rye at Abu Hureyra fits with the cool conditions of the late Pleistocene, but it would have been scarce because of the absence of suitable soils. *Polygonum/Rumex* gathered from the flood plain would have been a more reliable source of food than rye, the former being less affected by drought thanks to the water table, which was near the surface.

The Younger Dryas can be discerned from lake level changes, diatom analyses, and stable isotopes (Roberts *et al.* 2001). It was cooler and drier than today. The aridity may have been offset because low temperatures would have meant less evaporation and transpiration. *Pistacia*, grasses, and oak were exploited (van Zeist and Bakker-Heeres 1986, Willcox *et al.* 2009), so these resources were still available despite climate deterioration. Flood-plain species, which were less affected by the harsh conditions, made up an important part of the subsistence food plants at sites dating to the Younger Dryas.

The early Holocene is characterized by an increase in both temperature and rainfall. Tree species such as *Pistacia atlantica* were expanding in the Near East (Rossignol-Strick 1999) and this can be seen on the Euphrates valley sites by the high frequencies of *Pistacia* and *Amygdalus* charcoal and their fruits at Jerf el Ahmar and Dja'de (Hillman 2000, Willcox 2002b). As we have seen, cultivation appears to have been establishing itself during this period and more favorable climatic conditions may have facilitated this. But there is another climatic factor that may have contributed, the advent of more climatically stable conditions. It appears that at the beginning of the Holocene there is a reduction in short-term climatic variability. This has been identified from ice-core data, which show that the amplitude of oxygen isotope oscillations was high during the late Pleistocene and was reduced during the early Holocene (Figure 4.5). This implies that the Holocene climate was more stable with less short-term variation. It has been argued this stability may have helped in establishing cultivation during the PPNA in northern Syria (Willcox *et al.* 2009) between 11,500 and 11,000 BP. Founder crops of barley, single-grained einkorn, emmer, lentil, and pea began to be cultivated on Euphrates sites. Shortly afterwards new crops appear: faba beans, chick peas, and figs (see Table 4.1), having been introduced from elsewhere. Barley appears to have replaced rye, which could not tolerate the higher temperatures of the early Holocene.

Finally, a number of scholars agree that theoretically stable climatic conditions at the beginning of the Holocene were an important factor which allowed cultivation to develop into a reliable subsistence economy (Willcox 2000a,b, Richerson *et al.* 2001, Feynman and Ruzmaikin 2007, Hoek and Bos 2007). The Euphrates sites provide the demonstration of this through a direct correlation between the advent of stable climatic conditions and increased use of cultivation (Willcox *et al.* 2009).

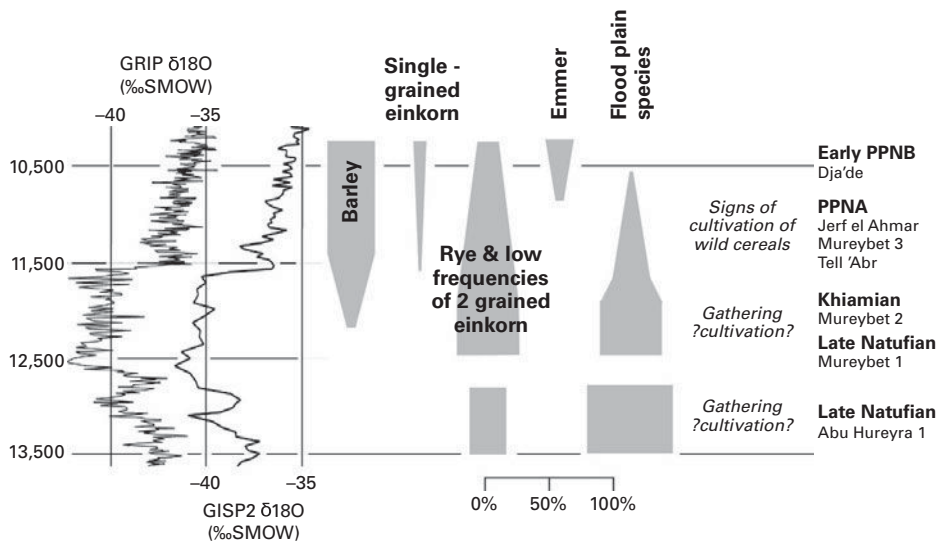


Figure 4.5. Approximate changes in the frequencies of the most common wild food plants from sites before the appearance of morphological domestication in the Euphrates valley in northern Syria, compared to the oxygen isotope curve (adapted from Hoek and Bos 2007, with their permission, and Willcox 2009). Rye is common during the late Pleistocene; it was used with small-seeded flood-plain species and goes out of use with the warmer conditions of the Holocene when barley and emmer become frequent. The amplitude of the oxygen isotope oscillations is high in the late Pleistocene, indicating unstable climatic conditions. With the Holocene the amplitude is less, indicating more stable conditions, which would allow cultivation to become a reliable means of subsistence. The break in the bars is because the archaeobotanical sequence is not continuous.

7

Conclusion

The archaeological sites examined here cover a period of more than 3,000 years, during which there were significant cultural developments and the first signs of cultivation. If small-scale cultivation occurred sporadically during the late Pleistocene, it may not have been sustainable because climate conditions were too unreliable for farming. Our archaeobotanical evidence suggests that the advent of stable climate conditions coincided with increased use of cultivation and may have facilitated its development into a sustainable economy when founder crops like barley, followed by emmer and then chickpea and faba bean, were brought into cultivation in the Euphrates area. The arrival of these new crops coincides with spectacular cultural developments. These are illustrated by the contrast between the humble Natufian dwellings at Abu Hureyra, which were mere shallow pits less than two meters in diameter, and the Khiamian houses at Tell Qaramel, which were constructed in stone and were several meters in diameter. By the PPNA large communal buildings were built at Tell 'Abr, Jerf el Ahmar, and Mureybet. The “kitchen” discovered at Jerf el Ahmar (Willcox 2002b) demonstrates a material investment in food preparation. Were these

developments a consequence of cultivation? This is not so easy to answer if we take into account Göbekli Tepe (Schmidt 2006) with its huge standing-stone circles. At present there is no evidence for cultivation at this site, although at present very few charred remains have been recovered. However it may not be coincidence that Göbekli Tepe is situated close to areas with the most extensive wild cereal stands.

Gathering and cultivation of wild cereals probably occurred simultaneously over a long period, which is why we see no sharp division from one economy to another, the transition being extremely gradual and episodic. Small-scale cultivation leaves little or no trace. The incentive to cultivate on a large scale could have been due to multiple factors, but the overriding factor would be difficulty in accessing wild stands or lack of sufficient quantities. Wild lentils, which are ubiquitous on early sites, may have been cultivated at an early date because of the rarity and the diminutive size of wild stands. Even when cereals and pulses were regularly cultivated, seed may have occasionally been obtained from wild stands and as long as this practice persisted any domestication traits which might appear would not be fixed in the population. The fixing of these traits and the establishment of a morphologically domesticated population would only occur when intensive cultivation was practiced exclusively and on a large scale.

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5 New Archaeobotanical Information on Plant Domestication from Macro-Remains: Tracking the Evolution of Domestication Syndrome Traits

Dorian Q. Fuller

1 The growth of archaeobotany

Archaeobotany is the specialist study at the frontier of archaeology and plant evolution. By the study of preserved plant remains from ancient human sites, archaeobotany provides evidence for use of plant resources by past cultures but also provides a record of datable ancient remains from which to document trends in the morphological evolution of crop species. As the available archaeobotanical data grow (Figure 5.1) it becomes increasingly possible to look comparatively at the trends in crop evolution, although we are still at an early stage in such research. The paper will explore some preliminary syntheses of such data, organized around a few traits of the “domestication syndrome” that are best documented in archaeobotanical macro-remains. In this exploration we focus on domestication as morphological adaptation on the part of plants, which results from the impact of human behaviors, represented by the term cultivation.

An adaptive syndrome of recurrent traits associated with cereal domestication was laid out by Jack Harlan, with his colleagues De Wet and Price, in 1973. Drawing mainly on comparative field observations of crops, their weedy races, and wild progenitors, this paper proposed both the morphological adaptations of crops and the selective pressures of human cultivators that were expected to select for them. These features were later incorporated into the taxonomically broader “domestication syndrome” of Hammer (1984). It is usually inferred that conscious intent on the part of cultivators was not necessary to explain the evolution of these traits, but rather these represented adaptation via natural selection to the anthropogenic environment of the cultivated field. As such, most domestication traits have been assumed to evolve by unconscious selection (e.g., Heiser 1988, Zohary 2004, Purugganan and Fuller 2009). Later in this chapter,

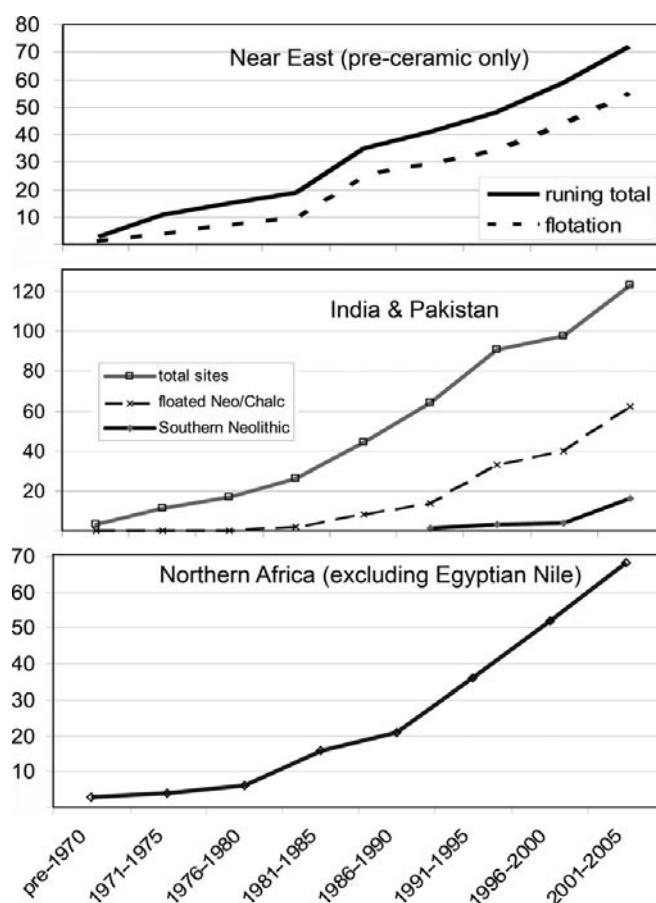


Figure 5.1. Charts of the quantitative growth of archaeobotany, indicating the cumulative number of published archaeobotanical reports in five increments. The top chart shows pre-ceramic Near East (after Fuller 2008a, based on data from S. Colledge). The middle chart shows India and Pakistan, with additional curves for the Neolithic/Chalcolithic and the Neolithic of Southern India (author's database). The bottom chart shows growth in northern and western Africa (excluding the Egyptian Nile) (after Fuller 2008a, data from Pelling 2007).

through a consideration of melon domestication, I will suggest that some cases of conscious, intentional selection may differ from typical domestication processes by being faster.

At the time that Harlan *et al.* wrote that paper, and Harlan (1975, second edition 1992) prepared the first edition of his *Crops and Man* reference book, archaeobotany was still in its infancy. While some archaeobotanical evidence was available to illustrate some early crops, and to confirm, in broad terms, the geography of domestication inferred from wild progenitors (also Zohary 1969, Zohary and Hopf 1973), the available evidence was rather inadequate for documenting the processes of morphological evolution at a population level.

As systematic archaeobotany, using collection methods of flotation, and where appropriate wet-sieving, has taken hold around the world, the available archaeobotanical data set of macro-remains (grains and chaff) has grown rapidly (Figure 5.1). In the Near Eastern data, we also see clearly that since the 1960s flotation has become standard and therefore systematically collected data have become more common. A similar trend is true for Africa but is complicated by the use of intensive dry-sieving in several dry regions, including the Western Desert of Egypt and rock shelters in Southwest Libya. This same trend appears again in India, but it should be noticed that in some subregions, such as South India, archaeobotanical data have only become available quite recently, providing for postulation of an additional potential center of crop domestication (Fuller *et al.* 2004, Harris 2005, Barker 2006). This growth of archaeobotanical data was accompanied by the maturation of this field of study, with the adoption of systematic collection and study methods and the growth of communities of specialists replacing earlier generations of avocational botanists who dabbled in this research (Fuller 2002, 2008a).

In the past decade or so it has become possible to begin to document archaeologically the evolution of the domestication syndrome, at least for a few better-documented crops and regions (Fuller 2007). We are able to suggest something about the rates and orders in which different morphological traits in different crops evolved. The present chapter will review and summarize what we know about these processes, especially in Asia and Africa, with some comparisons to North American data.

2 The evolution of nonshattering cereals: the case of wheat and barley

For many researchers (e.g., Helbaek 1960, Zohary 1969, Hillman and Davies 1990, 1992, Harris 1996, Zohary and Hopf 2000) dependence upon the human farmer for seed dispersal, owing to loss of natural seed dehiscence, is seen as the most important trait of domesticated seed crops. To quote Harlan:

Of all the adaptations that separate wild from cultivated cereals, the nonshattering trait of cultivated races is the most conspicuous. It is taxonomically the most diagnostic in separating domestic subspecies from spontaneous subspecies and is crucial in establishing the disruptive selection that effectively maintains separation of the two kinds of populations. Most of the seeds that shatter escape the harvest. (Harlan 1992:118)

In cereals this occurs by suppression of abscission at the abscission scars, such as the rachis attachment points in wheat or barley ears or the rachilla to spikelet base attachment in panicked cereals (rice and millets). The result is that, instead of shedding seeds when they are mature, a plant retains them, and they are then usually separated by the addition of human labor (threshing and winnowing). Higher yields can be produced because the farmer could wait until all, or most, of the grains on a plant have matured, whereas earlier harvesting would have had to

balance loss of grain through shedding, as they matured, with reduced yields through grains harvested immature (i.e., before spikelets have filled entirely). This would have been a particular problem with cereals such as wild rice, which has a long period of grain maturation, and which may have grown in wetland environments in which shed grains were lost (Fuller *et al.* 2007a, 2008, Fuller and Qin 2008). It was probably also a challenge for smaller-seeded millets, in contrast to large-spikelet cereals, like wheat and barley, which could be collected easily even if fallen (Kislev *et al.* 2004). The evolution of nonshattering would have occurred as a result of particular methods of harvesting that favored non-shattering (tough rachis) mutants in harvested populations, which were then sown (Hillman and Davies 1990, 1992). Harlan *et al.* (1973:314–315) and Harlan (1992:118) proposed that disruptive selection by human harvesting might be expected to strongly select for this domestication trait, leading to rapid fixation; and this postulate appeared to be borne out by extrapolation from experimental harvesting by Hillman and Davies (1990, 1992).

The empirical record of archaeology, however, appears to show this hypothesis to be false. Growing data sets for Near Eastern wheat and barley can be considered and these will be compared below to rice. In a compilation of data from five representative sites, three with einkorn wheat and two with barley, Tanno and Willcox (2006) suggested that cereal domestication might take millennia, perhaps as long as 3,000 years, while Weiss *et al.* (2006) accepted at least a 1,000-year period (also Feldman and Kislev 2007). A larger data set, based on nearly 5,000 einkorn spikelet bases (albeit many indeterminate) and nearly 5,000 barley rachises (Fuller 2007), indicates that there is a dominance of wild types through the Pre-Pottery Neolithic A (PPNA) and early Pre-Pottery Neolithic B (PPNB) but a dominance of domesticated types in the Late PPNB (see also Willcox, Chapter 4, this volume). These data also provide a crude approximation of the rate of change in the proportion of domesticated cereals, i.e., a rate at which nonshattering moved towards fixation (see Figures 5.2 and 5.3). The overall regional pattern indicates the replacement of entirely wild (shattering) barley with predominantly domesticated (nonshattering) barley by the end of the pre-pottery Neolithic periods, a domestication process taking at least 1,500 to 2,000 years, starting *c.* 9,500 BC. This can be inferred to be probably 1,000 to 2,000 years longer, if the process is regarded as starting from the Late Pleistocene cultivation inferred from the emergence of an arable weed flora at Abu Hureyra by 11,500 to 11,000 BC (Hillman *et al.* 2001, Willcox *et al.* 2008, see Willcox, Chapter 4, this volume). Although given that the evidence for cultivation at Abu Hureyra 1 seems to be focused only on rye, not barley and perhaps not wheat, it may be a “red herring” in terms of evidence for the beginnings of the sustained tradition of agriculture (see Willcox *et al.* 2009). Intriguingly, the domestication rate appears slightly faster in barley than in wheat (Fuller 2007). This is counterintuitive to conventional logic, by which cross-pollination slows down domestication (cf. Hillman and Davies 1990, 1992), since barley is often regarded as slightly more prone to cross-pollination (*c.*2%) than wheat (*c.*1%) (Hillman and Davies 1990, Morrell *et al.* 2005).

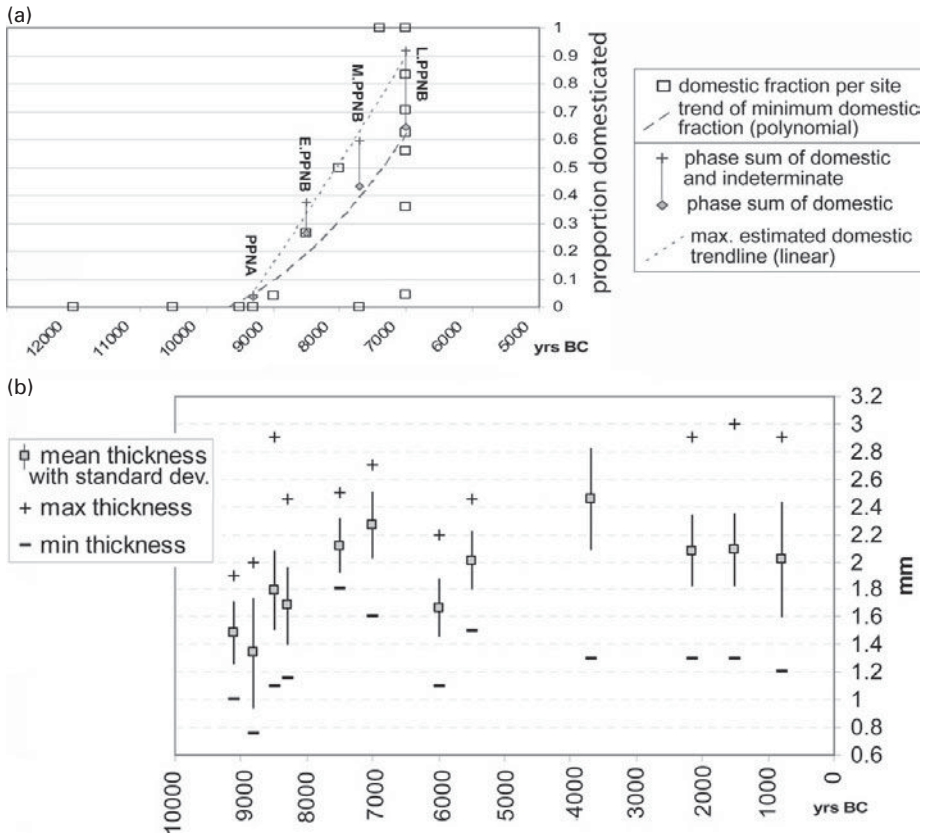


Figure 5.2. Charts comparing the change in domestication traits over time in the Near East for barley. (a) The percentage of domesticated (nonshattering rachis remains), through the pre-ceramic periods of the Near East, based on plotting minimum and maximum estimates of individual sites against a point estimate of site's median date (after Fuller 2007). (b) Trends in grain size shown as mean, standard deviation, and outlying minimum and maximum for individual site assemblages, plotted against a point estimate of site's median date (data compiled from various primary reports).

The evidence that allows us to track the change in frequency of the wild and domesticated morphological types brings out the issue of how we define domestication more precisely. It would be too simplistic to expect to find populations of 100% nonshattering cereals in early agriculture – especially given the likely persistence of wild progenitors as weeds. As an operational definition I have referred to dominance, meaning a clear, statistically significant majority of the nonshattering domesticated types over the shattering, wild type. Recent work on archaeological rice, for example, suggests that around 65%–70% nonshattering persists as the typical figure in agriculturally focused societies of the Late Neolithic (e.g., at Liangzhu, in Fuller *et al.* 2009, and at other unpublished sites). Once nonshattering types outnumber the wild, shattering type it becomes increasingly unlikely that chance drift or gene flow from the wild could push domesticates back

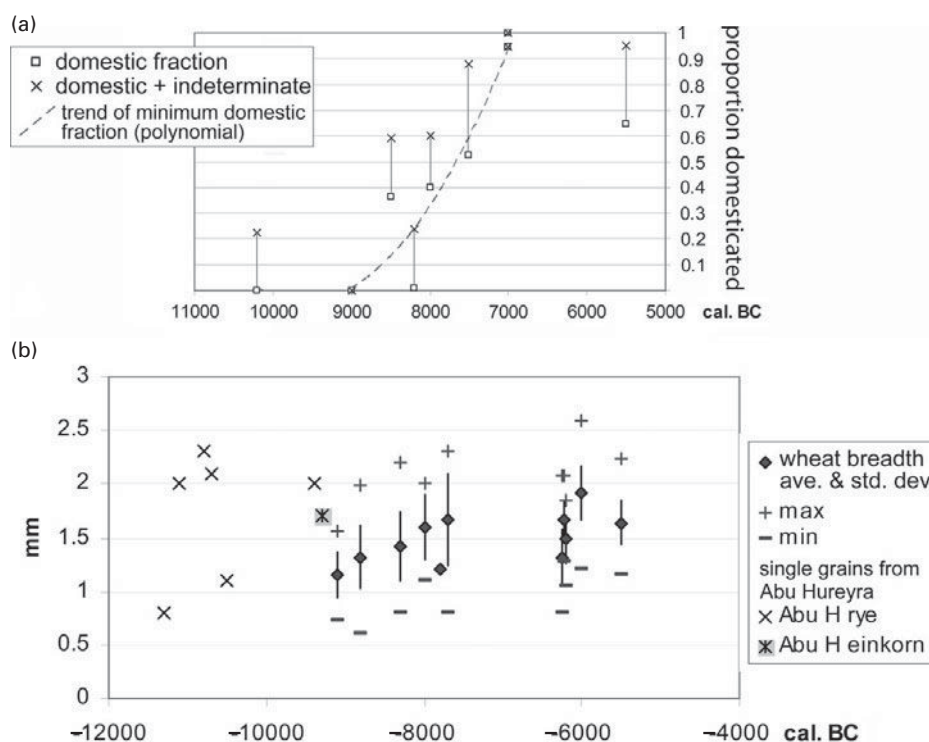


Figure 5.3. Charts comparing the change in domestication traits over time in the Near East for einkorn wheat (including some rye). (a) The percentage of domesticated (nonshattering rachis remains), through the pre-ceramic periods of the Near East, based on plotting minimum and maximum estimates of individual sites against a point estimate of site's median date (after Fuller 2007). (b) Trends in grain size shown as mean, standard deviation, and outlying minimum and maximum for individual site assemblages, plotted against a point estimate of site's median date (data compiled from various primary reports). Abu H, Abu Hureyra.

to a minority. Thus there is a majority-rule tipping point at which a population of crops can be regarded as domesticated.

While the predominance of domesticated-type (nonshattering) barley on most Near Eastern sites may have waited until *c.* 7,000 BC or after, by this period crops had dispersed already towards Europe, reaching mainland Greece and Crete (see Colledge *et al.* 2004, 2005), where fully domesticated forms dominate. Even earlier, by 8,400 to 8,000 BC, cereals had been transferred to Cyprus (Peltenberg *et al.* 2000), where domesticated chaff remains also dominate (although assemblages are very small) (Colledge 2004), although some wild barley was reported to be present in southern Cyprus at Pre-Pottery Shillourokambos (Willcox 2001, Colledge and Conolly 2006). This may suggest that local bottleneck effects sped up the domestication in dispersing crops that moved outside the region of the wild progenitor, or full domestication occurred during the less well-documented middle PPNB, or rates appear slower in the centers of origin because wild-gathered or

weedy barley continued to enter the archaeological record in this region of the wild progenitor. Certainly even in the late PPNB of the Near East there is inter-site variability in the proportion of wild barley rachis, which may relate to different degrees of continued reliance on gathering from wild stands. At Wadi Jilat 13, for example, specimens are almost entirely of wild type. This could be due to predominance of a gathering strategy at this site, which can also be suggested from a diverse range of other plant remains including evidence for wild edible tubers (e.g., *Cistanche* sp.) (Colledge 2001).

Models of the rapid fixation of domestication traits have assumed that strong directional selection on a single trait had been a predominant force (e.g., Hillman and Davies 1990, Zohary 2004), but current evidence means we need to take more seriously the dynamics of selection, which is acting on multiple traits, in small populations that are minute in relation to the vast surrounding population of wild progenitors. Drift is just as likely to associate deleterious as adaptive traits with nonshattering. Also, the new and small “invading” population of a crop should be expected to have a disproportionate rate of gene flow from the wild-adapted populations as a necessary part of the population genetics of invasions (see Currat *et al.* 2008). In terms of human behaviors, traditions of harvesting that had been honed for the gathering of shattering, wild cereals, may have been slow to change, and the shift to morphological domesticates would have incurred the added labor cost of threshing. It is thus something of an anachronism to presume that early cultivators would have acted in the first instance like farmers of later eras.

3 Comparing grain-size increase and nonshattering

The other trait often used for inferring domestication archaeologically is grain-size increase. It is well known that wild and domesticated cereal grains differ in size and this has been used to infer the domesticated status of cereals, already in the PPNA and the earliest PPNB, including sites from the Jordan Valley, the upper Euphrates in Syria, and the first settlements on Cyprus (Colledge 2001, 2004). However, given the slow rise of nonshattering forms, it can be suggested that the rate of evolution of larger grains may have been even faster (Fuller 2007). There is a growing morphometric database for wheat and barley from the Near East (Colledge 2001, 2004, Peltenberg *et al.* 2000, Willcox 2004). This indicates that wheat and barley grains increased in size starting in the PPNA and earliest PPNB. When data are considered representing populations of a given period, as plotted in Figures 5.2B and 5.3B, it can be seen that there is marked increase in grain breadth over the course of the earlier Pre-Pottery Neolithic (PPNA, Early to Middle PPNB). This occurs both through increasingly large maximal size ranges but also by elimination of the smallest grains from populations, but it remains the populational trend over time that compellingly suggests evolution. Subsequent to that in samples through to Bronze Age and Iron Age time there is no significant

trend for change in the size of grains on a population level, and thus we can conclude that the selection for increased grain size was part of crop evolution mainly in the early stages. The increase in nonshattering increases in tandem with increasing grain size, but it does seem that increased grain size may have had a slight head start. Indeed, Hillman (2000:379–82) argued that a few plump rye grains from Late Pleistocene Abu Hureyra represented “domesticated” cereals (Figure 5.3B). Although this may not be true based on a definition that emphasizes nonshattering, it is plausible that some selection for increased grain size is already indicated from the very start of cultivation.

Nevertheless, an explanation of these data remains controversial. I take this to indicate evolution towards larger grain size during occupation of this site (Fuller 2007, also, Nesbitt 2004:39), whereas Willcox (2004) by contrast queries whether this is not just a product of better-tended cultivars (i.e., phenotypic plasticity) or the introduction of larger-grained varieties from elsewhere (also Willcox *et al.* 2008:322). This early change is indicated in seed width and thickness, but not in seed length. Whereas Willcox (2004) argues that this does not fit with evolution of larger grains under cultivation, I think that a comparative perspective indicates quite the opposite. As was hypothesized by Harlan *et al.* (1973), grain size should increase as a product of soil disturbance and deeper burial with cultivation (also, Harlan 1992:122). This evolutionary tendency has an established observational and experimental basis in seed ecological studies (e.g., Krishnasamy and Seshu 1989, Maranon and Grubb 1993, Baskin and Baskin 2001:214, Sadras 2007). As reviewed by Sadras (2007) there appears to be genetic constraint on an equilibrium seed size (see also Borrás *et al.* 2004), selected by evolutionary processes, while seed number tends to be more variable in response to immediate environmental conditions. Studies on rice and barley have estimated that the heritability of grain size is high (Kato 1990, Fox *et al.* 2006). Nevertheless, it is clear that multiple genes affect grain size, and these often may be linked to other changes in inflorescence architecture and fruiting. A gene has recently been identified that affects panicle and grain number, plant height and grain size (Shan *et al.* 2009). Other studies on rice have identified key recessive mutations that seem to affect grain width by affecting the size and rows of husk cells (Fuller and Sato 2008, Shomura *et al.* 2008); another recessive mutation causes longer grains and higher grain mass (Fan *et al.* 2006). Similar mechanisms can be expected in wheat and barley. Although both size and number of seeds have a certain amount of plasticity, the relatively less plastic trait of seed size is more likely to have shown the directional change associated with early cultivation as a result of selection for genetic change. Because a larger number of potential genes contribute to grain size increase, the likelihood that a mutation in at least one of them should arise should be greater than that of mutation at single-locus traits such as nonshattering.

However, rather than seeing this as a single directional process, we must consider the likelihood that there were differing selective thresholds that acted on grain size (and multiple contributing genetic loci) at different times. This is

suggested by comparative examples, such as West African pearl millet or some pulses in which there was a lag between domestication and any appreciable increase in seed size (Fuller 2007, see below).

4 Chinese rice: a parallel case?

Systematic collection of archaeobotanical evidence directly bearing on rice domestication is quite recent, but a body of data on nonshattering is now available. The recognition of the potential for study of rice spikelet bases for determining the presence and quantities of wild-type shattering for domesticated-type nonshattering rice was recognized in the mid 1990s by Thompson (1996, 1997), and the recovery and study of some rice spikelet bases followed in medieval Mali (Fuller 2000) and Bronze Age Japan (Hosoya 2002). Quantified data from South China have only been studied more recently, including a compilation of *c.* 300 specimens from three sites by Zheng *et al.* (2007) and the author's work at Tianluoshan on more than 2,600 spikelet bases (Fuller *et al.* 2009, 2011), and emerging data sets from additional sites in this region (Fuller and Qin 2008; Fuller *et al.* 2010). There have been some issues regarding the establishment of morphological criteria on which to judge domestic/wild status, with the domesticated type of Thompson (1996, 1997) differing from that of Zheng *et al.* (2007, also Liu *et al.* 2007). Three clear categories can be recognized, including one that is likely immature (Fuller and Qin 2008).

Although current evidence does not allow us to identify the beginnings of pre-domestication cultivation, we have robust evidence for the mid to late part of the sequence of evolution of domesticated rice. Early and middle levels of the site of Tianluoshan, dating from *c.* 4,900 to 4,600 BC, have provided *c.* 2600 spikelet bases, indicating an increase from *c.* 27% to 35%–39% domesticated types through three sub-periods (Figure 5.4). This sequence also shows an increase in the proportion of rice and probable rice weeds as an overall proportion of the assemblage relative to wild-gathered staples such as acorns, *Euryale ferox* seeds, and *Trapa* water chestnuts (Fuller *et al.* 2009, 2011). Metrical data on rice from Tianluoshan fit with those of contemporary sites in being wider than measured populations from the early levels of Kuahuqiao, but still smaller than those of later assemblages towards the end of the Fifth Millennium BC or the early Fourth Millennium (Figure 5.4). Two factors contribute to the increasing average and upper range of grain populations: on the one hand, genetic selection for larger grains, and, on the other hand, a reduction in the proportion of immature spikelets harvested with smaller, unfilled grains (Fuller *et al.* 2007a, 2008). As with einkorn and barley in the Near East, grain size and nonshattering in rice evolved gradually in East Asia over more than 2,000 years, but it remains unclear which aspect of the domestication syndrome began to evolve first. Later sites in the region, Chuodun and Caoxieshan (4,200 to 3,900 BC), provide evidence for artificial field systems for wetland cultivation, i.e., paddy fields (Cao *et al.* 2006), and lack evidence for a

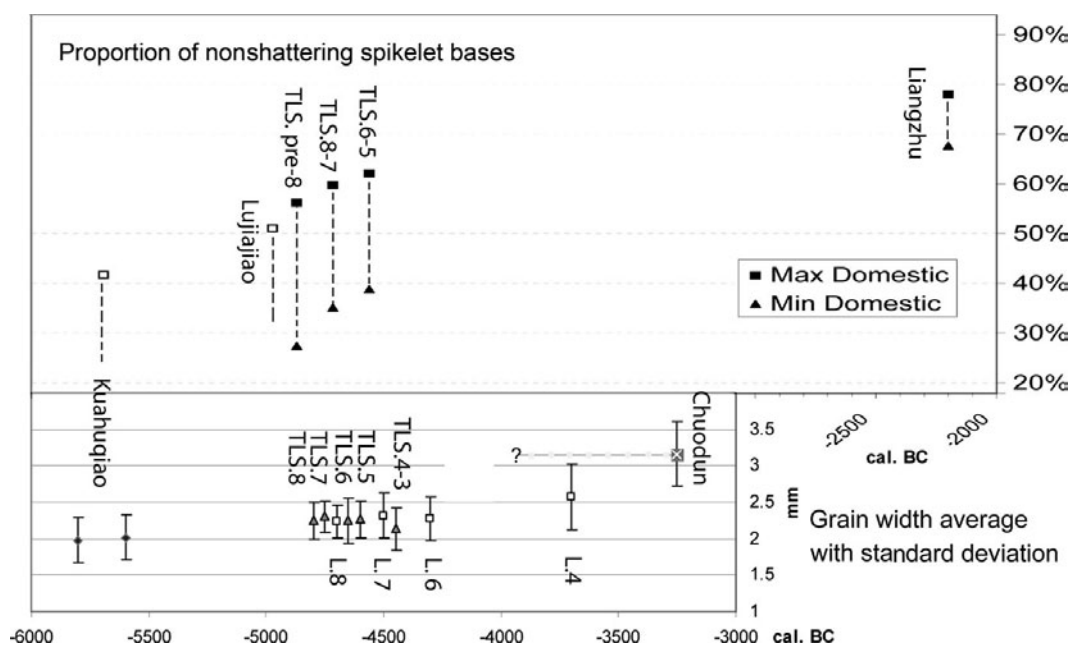


Figure 5.4. Charts comparing the change in domestication traits in Asian rice. (A) Estimated percentage of domesticated (nonshattering rachis remains), based on two bracketing estimates: minimum percentage observed nonshattering, and 1–% observed wild (Zheng *et al.* 2007, Fuller *et al.* 2009). (B) Trends in grain size shown as mean, standard deviation, starting at the left from the early and late periods at Kuahuqiao (based on data compiled in Fuller *et al.* 2007a, with additional data from Tianluoshan). TLS, Tianluoshan, with stratigraphic layer number; L, Longqiuzhang, with layer number; Chuodun measurements have been conservatively dated to the early Liangzhu phase since the paddy-field features at this site are overlain by Liangzhu levels.

significant reliance on acorns, suggesting that reliance on agriculture had taken over by c. 4,000 BC (Fuller *et al.* 2008).

5 An alternative case: African pearl millet

In the case of pearl millet, we have some metrical data from West Africa from which to examine grain size change during and after domestication (Figure 5.5). Pearl millet domestication is evident from ceramic impressions of pearl millet chaff that include the stalk, which are present by 1,700 to 1,500 BC in Mauretania (Amblard and Pernes 1989, MacDonald *et al.* 2003, Fuller *et al.* 2007b), and slightly later in Nigeria (Klee *et al.*, 2000, 2004), and there is new early evidence from the Tilemsi valley as early as 2,500 BC (Manning *et al.* 2011). While early grain assemblages, from 1,700 BC, show the subtle change towards domesticated grain shape, becoming apically thicker and more club-shaped (D'Andrea *et al.* 2001, Zach and Klee 2003), a major increase in seed size appears

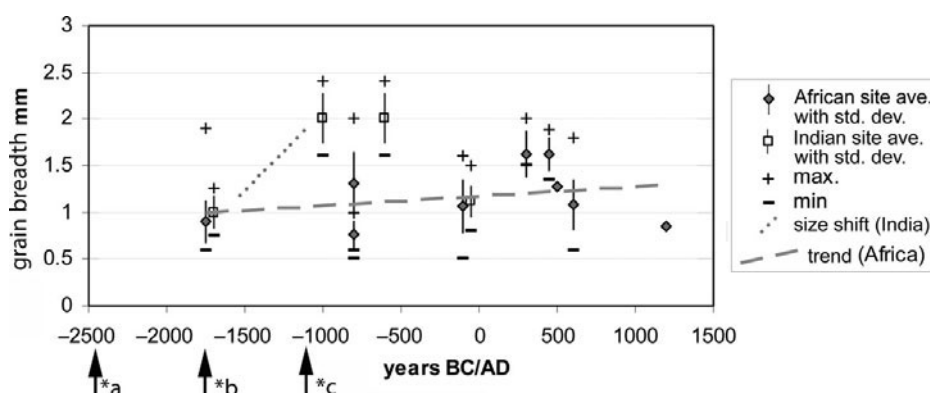


Figure 5.5. Archaeobotanical data for the evolution of domesticated pearl millet (*Pennisetum glaucum*), indicating grain-breadth measurements (mean and standard deviation, maxima and minima) for measured archaeological populations, plotted against approximate median age (data as compiled in Fuller 2007). Early and rapid trends for size increase in Indian populations are indicated by dotted lines, the more gradual trend in African populations is represented by a linear regression (dashed line). African sites from left to right: Birimi, Kursakata, Jarma (early, mid), Qasr Ibrim, Arondo, Jarma Late, Gao. Indian sites from left to right: Surkotada, Narhan, Nevasa; note the apparently earlier evolution of large grains in India. Arrows indicate archaeologically documented domesticated (nonshattering) populations based on impressions in pottery: a, Tilemsi valley (Manning *et al.* 2011); b, Dhar Nema (Fuller *et al.* 2007b); c, Ganjiganna (Klee *et al.* 2004).

delayed. Early West African populations, as well as those introduced to Gujarat, India by c. 1,700 BC, appear small, within in the wild size range. By contrast, rather later seeds of a North Indian (Gangetic) population from Narhan are markedly larger, suggesting selection for larger-grained pearl millet by 1,400 to 1,000 BC. Meanwhile in Africa there was a more gradual trend towards larger grain sizes, with some larger populations by the early first millennium BC and more by the later part of that millennium or the early centuries AD. From the more rapid increase in size on arrival in the Ganges plain in India, where mung beans also show a similarly timed size increase (see below), it can be hypothesized that size increase was driven by a similar selection pressure, such as deeper seed burial due to the introduction of ard tillage (Fuller and Harvey 2006, Fuller 2007). In the context of Africa it may be other forms of agricultural intensification which drove the later millet grain-size increase in some regions, although it was previously suggested (Fuller 2007) that large-grained forms evolved in regions with animal tillage, such as Nubia or Southwest Libya, and might then have dispersed back to sub-Saharan West Africa. Another issue of particular relevance to pearl millet is the balance of selection for more seeds versus the selection for larger seeds, for which there are apparent trade-offs. While at present we have enough data to outline the broad pattern of change in pearl millet, further research is needed to explain this pattern.

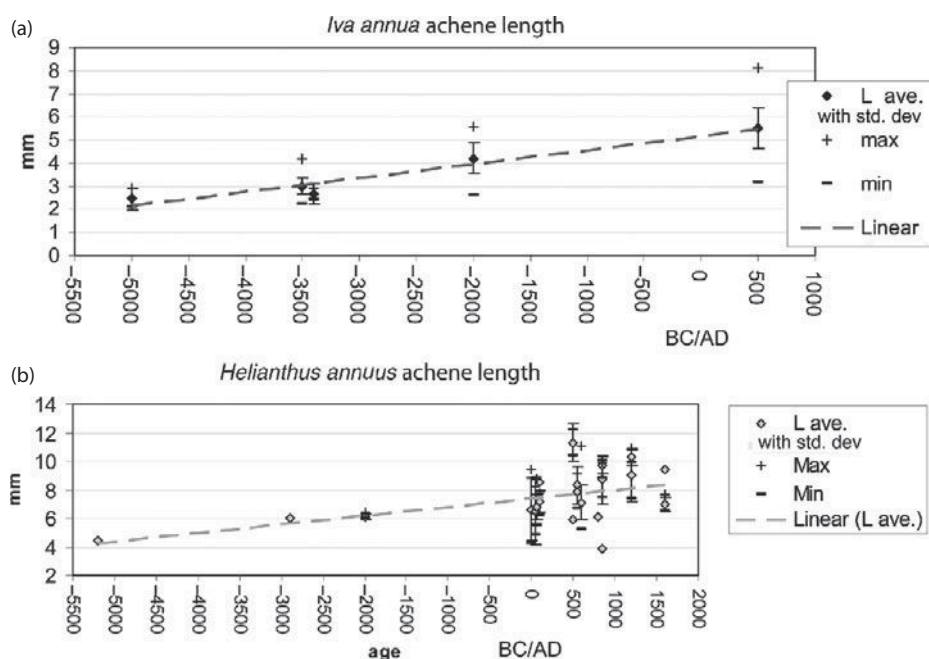


Figure 5.6. Metrical data of achene length (L) plotted against time for two North American domesticated Asteraceae, *Iva annua* and *Helianthus annuus*. Data from Asch and Asch (1985); see also Smith (1992:42).

6 Some comparisons from eastern North America

Two of the cultivars of the putative Eastern Woodlands center of domestication in North America have documented evidence for seed size increase, namely sunflower (*Helianthus annuus*) and the now extinct domesticated form of *Iva annua* (Smith 1992, 2006). Widely available data for these taxa (Asch and Asch 1985) reflect this process. When plotted as means and standard deviations against estimates of median age, like species considered above, trends towards size increase are clear (Figure 5.6). Significant size increase related to domestication can be estimated to have taken up to c. 1,500 years in *Iva* (between 3,500 and 2,000 BC), while in sunflower it was a very slow and gradual process, which may have begun already between 5,000 and 3,000 BC but is clear by about 1,500 BC (cf. Smith 1992).

7 Contradictory patterns in pulses

Pulse crops do not appear to show the same pattern of early and marked seed-size increase. A lag between domestication and any appreciable seed-size increase appears to be the case in Indian *Vigna* spp., i.e., mungbean and urd bean (Fuller and Harvey 2006, Fuller 2007), West African *Vigna unguiculata* (D'Andrea *et al.* 2007), and possibly soybean (cf. Crawford and Lee 2003, Fuller and Zhang 2007,

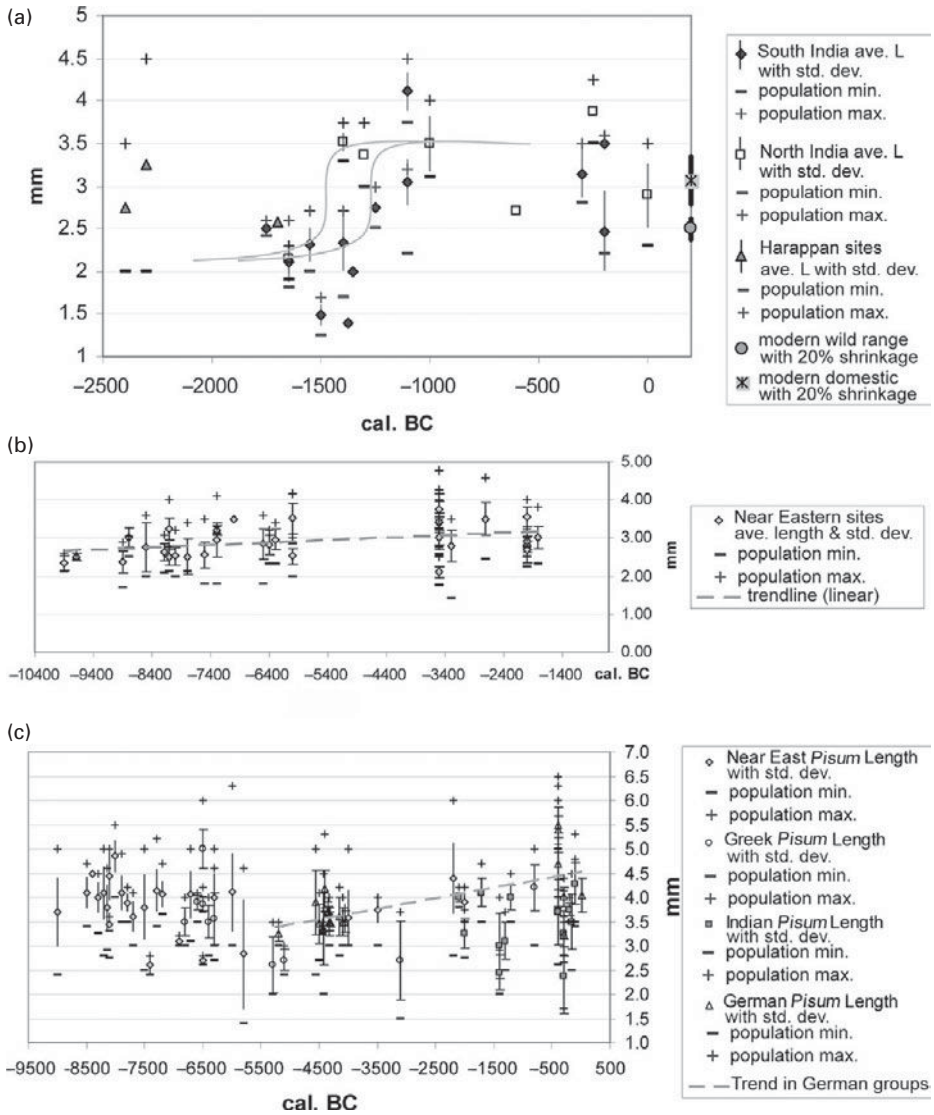


Figure 5.7. Metrical data plotted against time for selected pulse crops. (a) Mung beans from South Asia; (b) lentils from the Near East (middle); (c) peas from various regions of the Old World (bottom). Compiled from many primary data sources, summarized in Fuller and Harvey (2006) and Jupe (2003).

Zhao 2007). This may suggest that a higher selective pressure was needed to cross the threshold into big-seeded pulses; a threshold inferred by Fuller and Harvey (2006) to be ploughing (ard tillage). When plotted as a time series, it can be seen that South Indian *Vigna radiata* seeds increase markedly in width between 1,400 and 1,000 BC (Figure 5.7a). This period correlates with the end of the South Indian Neolithic and the transition to the Iron Age, which witnessed increased social complexity as well as the intensification and diversification of agriculture

(Fuller *et al.* 2007c). In this period we might expect the beginnings of arid tillage. In contrast, evidence from sites in the Ganges basin suggest an early seed-size increase in *Vigna*. The earliest Gangetic finds of this species suggest that this species was introduced (probably from South India) in the early second millennium BC as a small-seeded crop, and size change was marked by c. 1,400 BC, suggesting a slightly earlier shift to large seeds in Gangetic populations than in South India. As with South India, this can be suggested to correlate with a period of cultural change (the Chalcolithic transition) towards more hierarchical societies presumably with more intensive agriculture. This period also saw the adoption of textile production and fiber crops (cotton and flax) (see Fuller 2008b).

In Near Eastern lentils, size change appears to have been much slower and more gradual than in the cereals, without a clear leveling off after the Neolithic (Figure 5.7b). This may suggest an initially weaker selection, but may also indicate that seed size is more plastic in pulses, and that there were numerous local equilibrium sizes selected in different times and places.

In peas (*Pisum sativum*) a directional trend in seed size increase is even harder to see, although there is certainly increasing diversity in size between measured archaeological populations (Figure 5.7c). Nevertheless over the course of the PPNB (8,500 to 6,000 BC) there does appear to be a trend for larger seeds, judging by assemblage maxima, but there is no clear trend in assemblage averages. This suggests that early cultivation provided a context in which seed size could be more plastic and larger forms could occur, but there was no clear selection pressure, and it is unclear whether this represents phenotypic plasticity or increased genetic variation in seed size. The very small seed sizes from some populations, such as some from Neolithic Greece and later in India, may suggest that in some local environments smaller-seeded populations had an advantage: the balance between yield increases through seed size and seed number may have differed under various cultivation regimes, and whether use was as a dry pulse or a green seed. Nevertheless, if only the measured populations from Germany are taken into account there is a clear trend towards increasing size from the Early Neolithic onwards (Figure 5.7c), which might be suggested to relate to increasingly intensive field agriculture and the introduction of ards by the Late Neolithic (Sherratt 1997:230–1).

There is thus no recurrent pattern in the evolution of seed size in pulses. This may have something to do with the diversity of cultivation regimes to which pulses were subjected, e.g., whether they were tended in small garden plots more like vegetables or sown in single-species fields, or intercropped with cereals. The necessarily strong selection for the loss of wild-type germination inhibition in pulses may also have had pleiotropic effects on seed size.

8 The reduction of germination inhibition

Domestication normally involved the loss of germination inhibition. This may be the key trait in allowing species with highly dormant seeds, such as pulses

like the lentil, to be cultivated successfully (Ladizinsky 1987). While this change is associated generally with changes such as the thinning of seed coats, the lightening of seed-coat color, and the loss of rugae or papillae, and such traits can be documented in parallel across many families, genera, and world regions, these are difficult to detect archaeologically. Detailed studies are only available for a few species. One challenge is preservational: seed coats are often not preserved on charred pulses. This is clearly the case with Indian *Vigna* spp., for example (Fuller and Harvey 2006). Even when preserved there is no guarantee that seed coat thickness is informative for all species. In Near Eastern pulse crops, for example, Butler (1989, 1990) was able to document clear morphological differences in the seed coats of wild and domesticated peas, but not of lentils, chickpeas, or species of *Vicia*, where morphological variation falls along a spectrum from thicker (and sometimes ornamented) seed coats in wild populations and some cultivars, to thinner, smooth forms in other cultivars.

Those species which have been best documented are New World *Chenopodium* domesticates (e.g., Smith, 1989, 1992, 1995, Bruno and Whitehead 2003, Bruno 2006). In a classic case of the fossil record (archaeobotany) identifying an extinct crop, Smith (1989, 1992, 2006) tracked a marked decrease in seed coat thickness in *Chenopodium berlandieri* seeds from sites in the Eastern Woodlands of the United states between c. 2,500 BC and 1,500 BC. In addition to thinning seed coats, presumably linked to loss of wild-type germination inhibition, seeds tended to change shape and size, although wild-type forms persisted as weeds alongside the *Chenopodium* crop (Gremillion 1993). Bruno (2006) has developed a similar approach to studying South American *Chenopodium* domestication, although variation in seed coat thickness amongst wild species makes this more difficult, requiring the use of additional size and shape characters.

9 The increase in fruit size in cucurbits: evidence for conscious selection

Melon and squash domestication provides an example of a mode of domestication quite different from that of cereals and pulses. Melons, like other soft-stemmed fruits, possess elements of a recurrent domestication syndrome (Hammer 1984), such as larger fruit and seed size, loss of bitterness, and annuality. These may be plausibly attributed to a degree of conscious selection on the part of human cultivators rather than unconscious selection. Seed size may be readily documented through preserved macro-remains, and long *Cucurbita* seeds provide the earliest evidence for a morphological domesticate in Mesoamerica by c. 7,900 BC, although in this case it was suggested that seed size increased through unconscious selection because it preceded ring and peduncle thickening (Smith 1997). Nevertheless, presumably seed size and fruit size increase are linked allometrically, with conscious selection for larger fruits selecting for larger seeds as well; other traits

may represent a separate selective process. Distinctive phytoliths (micro-remains) from the rinds of *Cucurbita* also appear to be allometrically linked to fruit size (Piperno and Stothert 2003, Piperno and Pearsall 1998:194–5). Metrical data from such phytoliths provides evidence for the relative scale and rate of size increase in some early New World *Cucurbita* populations, such as probable *C. ecuadorensis* (Piperno and Stothert 2003). In this case phytolith measurements suggest a quite gradual trend in fruit size increase between 11,000 and 6,000 cal. BC. In this chapter, I will consider the Old World melon (*Cucumis melo*), and in particular new data for a comparatively rapid local domestication in the Lower Yangzte region.

The melon is inferred to have multiple domestications across its former wild range. Wild *Cucumis melo* L. subsp. *agrestis* occurs from Africa and the Near East, through Central India (Madhya Pradesh; western Jharkand and Chattisgarh), as well as in central and eastern China (Chakravarty 1959, Kirkbride 1993, Zohary and Hopf 2000, Akasi *et al.* 2002, Lu *et al.* 2006, Zheng and Chen 2006). Archaeobotanical evidence of apparently morphologically wild melon seeds from the Lower Yangzte in the mid-Holocene suggest an extirpation of wild populations there during recent millennia (see below). Zohary and Hopf (2000) accept at least two domestications, one focused on the Near East (Egypt?) and one on South Asia (the Indus?), but we can now document a likely (third?) domestication episode in Eastern China, as previously suggested by Walters (1989). A sub-Saharan African domestication, often suggested from modern genetic diversity (e.g., Kirkbride 1993, Akasi *et al.* 2002), lacks archaeological support: melon cultivars were present in Egypt, the Indus, and the Yangzte (by third millennium BC) before *any agriculture* was present in most of sub-Saharan Africa!

In recent years, melon seeds, usually waterlogged, have been recovered from eight archaeological sites for which metrical data are available (data from six sites published in Zheng and Chen 2006, two additional sites documented by this author). The earliest finds are 15 seeds from Tianluoshan dating from c. 4,600 BC (full archaeobotanical evidence in Fuller *et al.*, 2011). From close to 4,000 BC a few seeds are available from Chuodun and from c. 3,300 BC from Puanqiao (DQ Fuller & L Qin, unpublished data), while a series of melon assemblages from the third millennium to the early second millennium BC are collected in Zheng and Chen (2006). Based on modern domesticated melons, 5mm is a suggested minimum seed length for domesticated melons. The seed length data from lower Yangzte archaeological populations are shown in Figure 5.8, and it can be seen that populations are firmly within the wild size range from the fifth millennium BC to the mid-third millennium BC. Only at the sites of Tadi and Qianshanyang of the late third millennium BC is there marked increase in population averages, including seeds significantly above the 5mm threshold. This suggests domestication, and that this shift to larger seed (and fruit) size evolved rapidly, perhaps within a century around c. 2,200 BC.

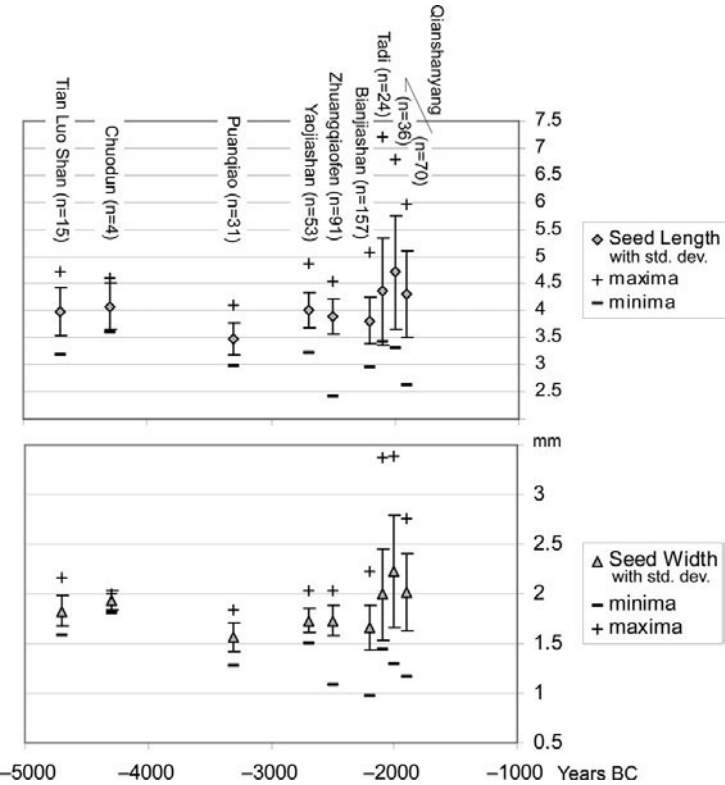


Figure 5.8. Metrical data on melon seed length and width from the Lower Yangzte, suggesting local rapid evolution of larger fruits and seeds in the Lower Yangzte, presumably under conscious selection. Plotted are means, standard deviations, and maximum and minimum values for seed length and seed width, against approximate median age of seed assemblages. Data from Zheng and Chen (2006) and DQ Fuller (unpublished: Chuodun, Puanqiao).

10 Conclusions

Domestication represents convergent/parallel evolution of adaptations to human cultivation and harvesting. But despite parallel results in terms of the domestication syndrome (Hammer 1984), not all species followed the same domestication trajectory. Table 5.1 summarizes the archaeologically documented domestication traits across a range of species, including those reviewed in this chapter and those for which published data are available, including North American domesticates (Asch and Asch 1985, Smith 1992, 2006), American *Cucurbita* (Smith 1992, 1997, Piperno and Pearsall 1998), and Japanese barnyard millet (Crawford 1983). What can be seen is much variation in the rates at which seed/fruit size increase occurred. These range from rapid, on the order of one or a few centuries, in fruits such as melons that were probably under conscious selection, and some pulses, to semi-rapid when size increase took

Table 5.1. Comparison of evolutionary rates of domestication syndrome traits across selected crops documented by archaeobotany

Crop [region of origin] (sources)	Traits	
	Semi-domestication	Domestication
	Seed size	Nonshattering Germination/ Seed-coat thinning
Poaceae		
Einkorn wheat [Levant] (see text)	Semi-rapid, <i>c.</i> 1,000 years	Slow <i>c.</i> 3,000 years
Barley [Levant] (see text)	Semi-rapid, <i>c.</i> 1,000 years	Slow <i>c.</i> 3,000 years
Rice [China] (see text)	Slow, <i>c.</i> 2,000 years, later rapid burst, <i>c.</i> 100 years	Slow <i>c.</i> 3,000 years
Pearl millet [West Africa] (see text)	Semi-rapid, <i>c.</i> 700 years (India after arrival), >1,000 years (Africa)	
<i>Echinochloa crusgalli/utilis</i> [Japan] (Crawford 1983)	Slow, <i>c.</i> 2,000 years	
Fabaceae		
Mung bean [South India] (see text)	Delayed, but rapid, <i>c.</i> 300 years	
Lentil [Near East] (see text)	Very slow/ delayed, with multiple local trends	
Pea [Near East] (see text)	Very slow/ delayed, with multiple local trends, <i>c.</i> 1,000 years (Germany)	Rapid (?)
Asteraceae		
Sunflower [North America] (Asch & Asch 1985, Smith 1992)	Semi-rapid <i>c.</i> 1,000–2,000 years	
<i>Iva annua</i> [North America] (Asch & Asch 1985, Smith 1992)	Semi-rapid <i>c.</i> 1,500 years	
Chenopodiaceae		
<i>Chenopodium berlandieri</i> [North America] (Smith 1992)	Semi-rapid(?)	Semi-rapid, <i>c.</i> 500 years
Cucurbitaceae		
Melon [China] (see text)	Extremely rapid <i>c.</i> 100 years	
<i>Cucurbita pepo</i> [Mesoamerica] (Smith 1997)	Semi-rapid (?)	
<i>Cucurbita</i> cf. <i>ecuadorensis</i> [South America] (Piperno and Stothert 2003)	Very slow and gradual	

around a millennium, as in Near Eastern cereals, pearl millet, and North American Asteraceae, or slow, where 2,000 years or more were needed, as in Asian rice, perhaps lentils and peas. In some taxa, such as cereals and perhaps North American crops, size increase seems to have occurred with the start of cultivation, while in taxa such as pulses and perhaps pearl millet, it was delayed until some later period.

This suggests, in turn, that certain factors in cultivation regimes interact with the inherent variability and genetic architecture of seed size traits within particular taxa in ways that are not uniform across taxa. It has been suggested that the size trait be regarded as “semi-domestication” as it is a quantitative population-level trait that is selected at some stage during human cultivation but not necessarily linked directly to key domestication traits, such as nonshattering (Fuller 2007). By contrast, nonshattering can be qualitatively determined on individual specimens. Seed size and other such traits constitute a kind of “soft” selection in relation to the cultivated environment and probably a high degree of within-population variability built on a multi-genic basis (Sadras 2007:132–3, Fuller and Allaby 2009). The differences between crops should be related to differing selective thresholds relating to the histories of cultivation of these species and the particular genetic architectures of grain-size traits. Archaeobotanical data then concur with the conclusions of Harlan (1992) and Heiser (1990:199) that it is “more likely that large seeds result from unconscious selection over a period of time”. Only in the cases of the most rapid change, like that of melons, does conscious selection seem likely.

Intriguingly the protracted fixation of nonshattering in cereals is paralleled across species (wheat, barley, rice) and regions (Near East and China), at a surprisingly similar rate of change (and thus coefficient of selection) (Purugganan and Fuller 2009). This is contrary to the accepted wisdom of strong selection and rapid evolution under “sickle pressure” (e.g. Wilke *et al.* 1972, Hillman and Davies 1990, 1992, Willcox 1999), leading to disruptive selection (Harlan 1992:118). Thus sickles as the main driving force are open to question (Fuller 2007). Indeed, in some regions like the Near East sickles clearly precede domestication by many thousands of years, while in other regions like the Yangtze valley of China sickles or harvesting knives appear absent until introduced from the millet zone to the north, after rice was already domesticated (Fuller 2007, Fuller *et al.* 2008). As suggested by Willcox *et al.* (2008) the recurrent bolstering of cereal store from wild stands also must have played a role. What seems to be clear is that disruptive selection appears to have not occurred or to have been very weak, and the role of balancing selection for wild-type adaptation and gene flow, even at low cross-pollination rates, needs to be taken into account (see Allaby *et al.* 2008). The pristine harvesting experiments of Hillman and Davies (1990), divorced from the real environments of the Near East, with gene flow, and concurrent selection for other domestication syndrome traits, were not an analogue for the Epipalaeolithic of the Near East. Lu (2006) has recently shown experimentally how weak sickle pressure would be in the context of harvesting (mature) wild Asian rice. Further

archaeobotanical evidence, real-world experiments, and extended biological systems simulations *in silico* (as per Allaby *et al.* 2008) are needed.

The cases explored in this chapter argue that we need to consider different aspects of the domestication syndrome separately, even different aspects of grain shape and size change. Nevertheless, there are cases of parallel trends seen in unrelated cereals and centers of origins which suggest that some of the same fundamental evolutionary processes were at work. Archaeobotanical evidence, in the form of macro-remains, provides one key line of research in documenting the domestication process.

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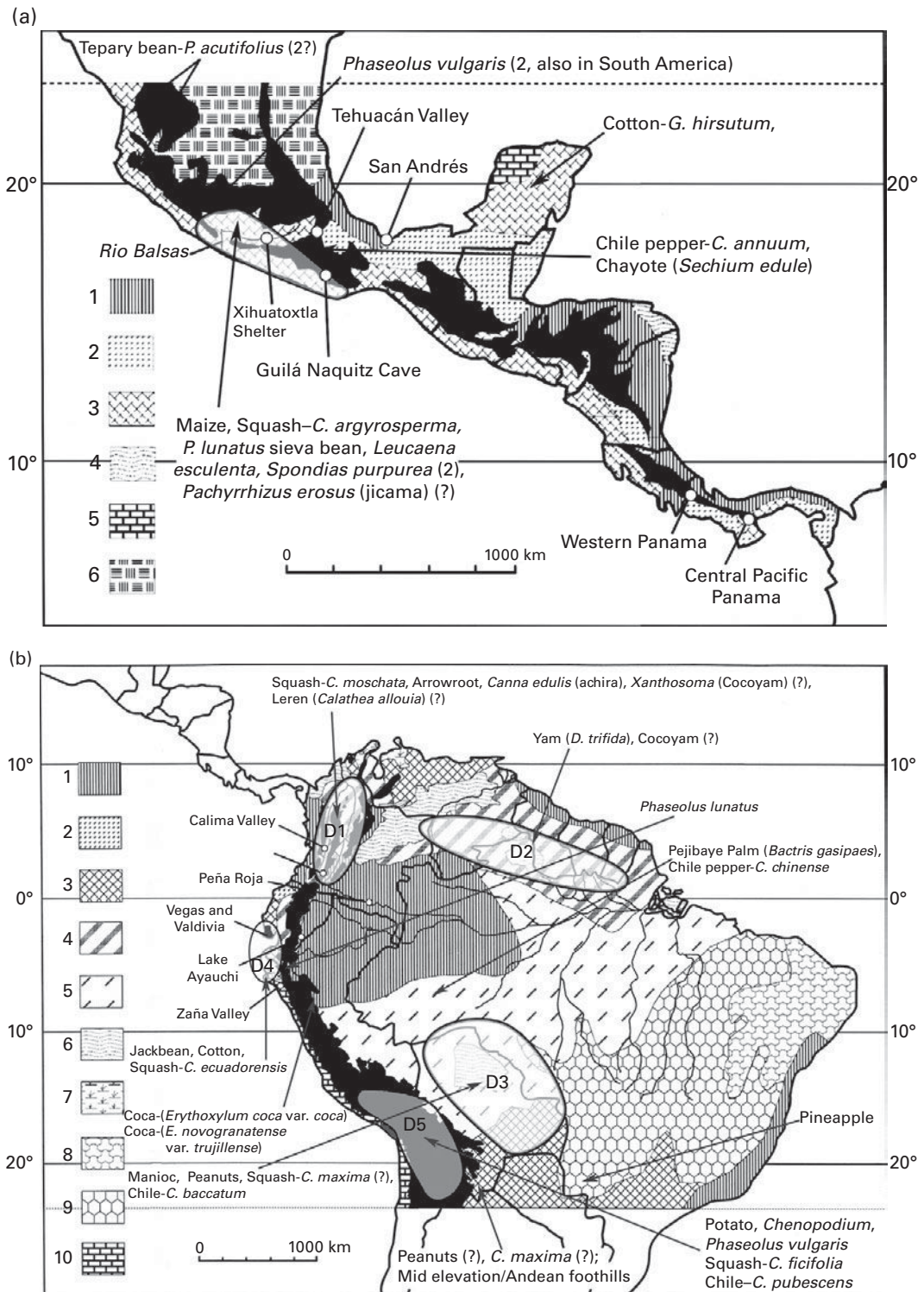
6 New Archaeobotanical Information on Early Cultivation and Plant Domestication Involving Microplant (Phytolith and Starch Grain) Remains

Dolores R. Piperno

Archaeobotanical information relating to early plant cultivation and domestication and derived from microfossil research is rapidly expanding. In this paper I review recent data, focusing on the lowland tropics of Central and South America and primarily on phytolith, starch grain, and where available, ancient DNA remains. New and important macrobotanical evidence is also discussed. I more briefly review recent developments in other regions of the Americas and the Old World, in order to provide a broader survey of microfossil contributions to early agriculture studies. Data generated during the past ten years impact old and newer debates concerning how and when important crop plants arose and spread, and when effective food production – defined as systemic cultivation that supplied stable and significant dietary inputs – began. Phytolith and starch grain applications provide information at various, fundamental levels of understanding ranging from basic identifications of wild and domesticated species, to the direct documentation of ancient diets through recovery from the calculus of human teeth, to the generation of data on the evolution of domestication genes in some major crops.

1 The geographic scenario of agriculture in Central and South America

Before reviewing archaeobotanical data it is useful to outline the geographic scenario of plant domestication in Central and South America, where the great majority of New World crops originated (Sauer 1950, Piperno and Pearsall 1998). [Figure 6.1\(a, b\)](#) provides a summary based on current archaeological, molecular, and ecological information. The maps will undoubtedly be subject to some future changes as well as further refinements, especially in South America where many



important root and other crops were domesticated. An important point to be stressed is that crop origins were more spatially diffuse than once thought. Particularly in South America, it is difficult in the light of current evidence to talk about single or a few nuclear areas/centers of crop domestication, a point that Harlan first brought to light many years ago (Harlan 1971). There appear to have been multiple areas of local domestication, including with different species of the same genus as occurred in squashes (*Cucurbita* spp.), beans (*Phaseolus* spp.), chile peppers (*Capsicum* spp.), and cotton (*Gossypium hirsutum* and *G. barbadense*). There were likely a number of local areas that saw nondomestication cultivation and protracted periods of pre-domestication cultivation. These early practices, involving plants that are persistently cultivated (a routine cycle of sowing and harvesting), but that do not acquire all or even some of the phenotypic traits typical of domestication for hundreds to thousands of years, are increasingly being documented in southwest and eastern Asia with major, early crops such as einkorn wheat, lentils, and rice (e.g., Weiss *et al.* 2006, Fuller 2007 and Chapter 5, this volume). The possibility of a similar beginning to agriculture in the New World, whereby domestication was a more complex and protracted process than once thought, and cultivated but still morphologically wild plants formed the basis for the first stable and effective food production systems, needs to be better explored (see Piperno 2011).

Another noteworthy pattern that emerges from the evidence is that most important lowland crops in both Central and South America were originally brought under cultivation and domesticated in the seasonally dry but not the ever-wet tropical forest. It appears that the interior of the Amazon Basin had little to do with the origins of major subsistence and other crops (e.g., Piperno and Pearsall 1998, Olsen and Schaal 1999, Matsuoka *et al.* 2002, Sanjur *et al.* 2002,

Caption for Figure 6.1 (cont.)

and palaeoecological sites in lowland and highland Central and South America with early (10,000 BP to 5,000 BP) domesticated seed and root crop remains. The numbers in parentheses after a taxon indicate that more than one independent domestication occurred. The possible area of origin for the sieva bean extends into the Pacific lowlands north of the oval area. The oval in (a) and those in (b) labeled D1–D5 designate areas where it appears that a number of important crops may have originated. See Piperno and Pearsall 1998 and Piperno 2006a,b for more details and sources used in the figure, and also Léotard *et al.* 2009, Chacón S. *et al.* (Chapter 14, this volume), Miller and Schaal 2005, Matsuoka *et al.* 2002, Kwak *et al.* 2009, Olsen and Schaal 1999, Sanjur *et al.* 2002, Hughes *et al.* 2007, Westengen *et al.* 2005, Wessel-Beaver 2000, Muñoz *et al.* 2006, Spooner *et al.* 2005, Rodrigues *et al.* 2004, Cross *et al.* 2006, and van Heerwaarden *et al.* 2011. Modern Vegetation Zone Guides for (a) 1, tropical evergreen forest; 2, tropical semi-evergreen forest; 3, tropical deciduous forest; 4, savanna; 5, low scrub/grass/desert; 6, mostly cactus scrub and desert. Black areas indicate mountain zones above 1500 masl. Modern Vegetation Zone Guides for (b): 1, tropical evergreen forest (TEF); 2, tropical semi-evergreen forest (TSEF); 3, tropical deciduous forest (TDF); 4, mixtures of TEF, TSEF, and TDF; 5, mainly semi-evergreen forest and drier types of evergreen forest; 7, thorn scrub; 8, caatinga; 9, cerrado; 10, desert. Black areas indicate mountain zones above 1500 masl. Modified from Piperno 2006b.

Westengen *et al.* 2005, Piperno 2006b, 2011). With regard to the primacy of lowland vs. highland origins of agriculture, the present evidence suggests that a number of lowland crops were cultivated and/or domesticated earlier than important highland species such as potato, *quinoa*, and *C. ficifolia* squash (Piperno and Pearsall 1998 and see below). However, more evidence, including from microfossil work, is needed from the highlands of Ecuador, Peru, and Bolivia to better document the chronology of food production emergence there. For example, recent data, discussed in more detail below, indicates that *Phaseolus* beans were brought under cultivation earlier than about 8,600 BP, by which time they had been dispersed into the lower western slopes of the Andes (Piperno and Dillehay 2008).

2 Major patterns of early Neotropical agriculture

Microfossils have provided important archaeobotanical data sets in lowland regions, especially for earlier time periods when macrofossil preservation in humid areas is very poor. The accumulated data demonstrate a number of consistent and broad trends. In every region that has been well studied the same or similar sets of crops persistently occur the earliest in phytolith and starch records, which come from securely dated stone tool residues and associated sediments from numerous sites (Figure 6.2) (see Piperno 2011, for a detailed review). In several cases, phytoliths (Piperno and Stothert 2003, Piperno 2006a) and most recently starch grains (Zarillo *et al.* 2008) have been directly dated. The earliest crops include: at least two species of squash [one probably native to northern South America (*C. moschata*) and the other to southwestern Ecuador (*C. ecuadorensis*)], maize, manioc, peanuts, and two now minor root species, arrowroot (*Maranta arundinacea*) and leren (*Calathea allouia*). These were some of the participants of the first crop complexes in the Neotropical lowlands. Arrowroot and leren, both grown for their starch-rich tubers, are now of minor importance in traditional Neotropical agriculture and appear to be disappearing from native agriculture in some regions, but they obviously played much greater roles at the beginning of agriculture.

Maize is now evidenced from starch grains and phytoliths in the Central Balsas River Valley of Mexico, its presumed cradle of origin, at 8,700 BP (Piperno *et al.* 2009, Ranere *et al.* 2009). Systematic archaeological foot surveys carried out in this region, combined with excavations and detailed phytolith and starch grain studies of stone tools and associated sediments, have revealed the following lines of information (Piperno *et al.* 2009, Ranere *et al.* 2009). By the beginning of the Holocene, the Balsas seasonally dry tropical forests were occupied by foragers who possessed ground-stone tool technologies dedicated to the preparation of a variety of native plant foods for consumption. Maize together with a species of squash, either *C. argyroperma* or *C. pepo*, more likely the former, were domesticated by 8,700 BP and at this time both crops were undergoing human selection for important traits such as softer, reduced glumes (maize) and softer fruit rinds

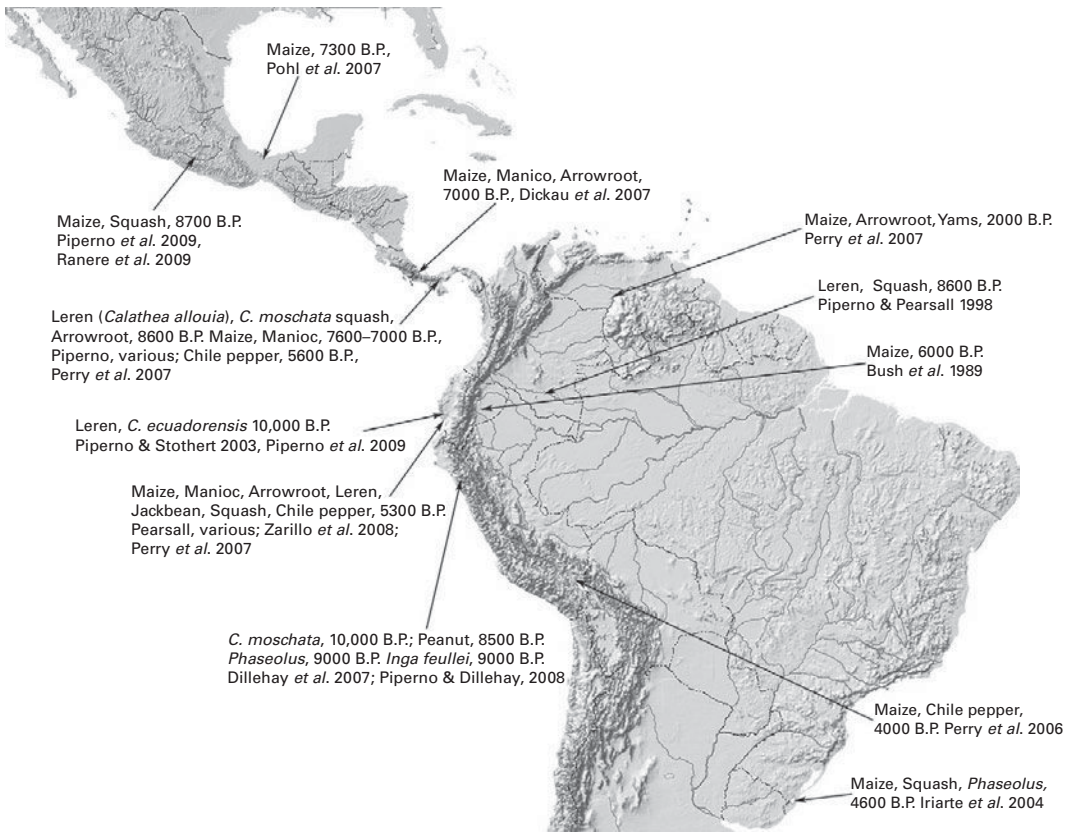


Figure 6.2. Early crop plants recorded from microfossil evidence, the areas where they occur, and dates of their appearance at various sites in Central and South America.

(squash). Multifaceted microfossil evidence from both archaeological and paleo-ecological settings also indicates that maize was dispersed into lower Central America by 7,600 BP (Piperno *et al.* 2000, Piperno 2006a,b, Dickau *et al.* 2007) and was well established in South America by 6,000 BP (Bush *et al.* 1989, Pearsall *et al.* 2003, 2004, Zarillo *et al.* 2008).

There is recent information from macrobotanical remains and starch grains indicating that a lowland species of squash native to South America (*C. moschata*) along with peanuts and manioc were dispersed into northern Peru by 10,000, 8,500, and 8,000 BP, respectively (Dillehay *et al.* 2007, Piperno and Dillehay 2008). This evidence is discussed in more detail below. Although it cannot be said for sure which and how many species were involved, chile peppers appear to have been well dispersed in Central and South America by 5,000 years ago (Perry *et al.* 2007). In some regions of the Andes and the South American lowlands where archaeobotanical investigations do not have a long history, microfossil applications have provided the first substantive empirical data on the incorporation of

maize, squash, beans, chile peppers, and arrowroot into local economies (Iriarte *et al.* 2004, Perry 2005, Perry *et al.* 2006). Moreover, recent starch grain work in Puerto Rico has revealed for the first time empirical evidence for root crops such as manioc, sweet potato, and cocoyam, all of which occur at 3,300 BP (Pagán 2007). Maize starch is also present.

In summary, everywhere that a significant amount of data has been generated, records show that both early and later lowland food producers were growing diverse mixtures of root, seed, and probably tree crops, making characterizations of prehistoric tropical farming as either seed crop- or root crop-based no longer valid. It is clear that some major crop species (e.g., *Cucurbita moschata* squash, manioc, peanuts, maize) were dispersed out of their original domestication areas by 8,000 years ago. Thus, the origins and initial dispersals of agriculture in the American tropics date to the early Holocene, about the same time as in the Old World, and several different regions and cultural traditions of the tropical forest can be identified as having been involved. Future investigations in southern South America (e.g., lowland Bolivia and southwestern Brazil), where manioc, peanuts, and other crops were originally taken under cultivation but where archaeobotanical research has not yet been applied, should reveal more important examples of early food production.

3 Other regions with microfossil data for early agriculture

The American tropical zone is one of several regions of the world where microfossil data have proved effective in studying the emergence and spread of agriculture. As in the Neotropics, a wide variety of different problems have been addressed. A detailed review of this corpus of work with regard to the phytolith evidence can be found in Piperno (2006a). Some noteworthy phytolith studies published since then are discussed here.

Phytolith evidence now places maize and squash in the northeastern USA (New York State) at 2,300 BP and 3,100 BP, respectively. This is 1,300 years earlier for maize and considerably earlier for squash than was recorded from previous studies in the study region based on macrofossil data alone (Hart *et al.* 2007, Hart and Matson 2008). The results come from directly dated food residues recovered from ceramic pots. In the case of maize, the evidence is even older than the oldest dated maize macrofossils in the eastern USA, suggesting that phytolith research (and likely starch grain analysis once this technique becomes routinely applied; see Zarillo and Kooyman 2006, Messner *et al.* 2008, Boyd and Surette 2010) will continue to result in revisions to the age of the dispersals of maize and other crop plants.

Phytolith applications in China are expanding at a particularly rapid rate, with a number of important issues under intense study. In a novel application, Lu *et al.* (2005) used phytoliths to identify the earliest noodles in China as having been made from common millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*),

not from wheat. The phytoliths were dated to about 4,000 BP, firmly establishing China as the original home of the noodle. Lu and colleagues then extended their millet research to earlier time periods in order to address the long-standing question of what was the earliest domesticated millet in northern China, the heartland of both the common and foxtail types. To study the issue, they first undertook a painstaking comparative analysis of inflorescence (glumes, lemmas, and paleas) phytoliths in modern wild and domesticated *Setaria* and *Panicum* (Lu *et al.* 2009a). They found a number of key diagnostic features of silicification in these structures that could be used to confidently separate the two genera, and moreover each domesticated species had characteristics distinguishable from their wild ancestors. They turned next to the important early Neolithic Chinese site of Cishan, where previous evidence was ambiguous in terms of which millet was present and had been grown first. The phytolith evidence strongly indicated that common millet was grown, stored in quantity, and commonly consumed 10,000 years ago, 1,600 years before foxtail millet appeared (Lu *et al.* 2009b).

Chinese phytolith studies are also contributing significant new information concerning the evolution of wetland rice agriculture in the lower Yangtze region (e.g., Jiang and Liu 2005, Itzstein-Davey *et al.* 2007, Innes *et al.* 2009). Previous research showed that phytoliths from rice husks can be identified to the genus, and that using statistical analyses, wild and domesticated species of *O. sativa* can be distinguished (see Piperno 2006a for a review). An important aspect of much of the most recent work is the combined, multiproxy archaeological and paleoecological (including pollen) applications that provide detailed data on the ecological contexts and consequences of early wet rice agriculture. The work has shown that rice cultivation began in the region around 7,800 years ago.

Phytolith research is gaining speed in Africa and other parts of the Old World such as south Asia where applications of the technique had been few in number. A long-standing question has been the date of appearance of a major exogenous crop, banana (*Musa*), on the African continent, where wild bananas do not occur. Phytoliths are well suited for studying this issue because the leaves and seeds of *Musa* and *Ensete* spp., the latter a close banana relative native to Africa and itself a major indigenous crop there, produce phytoliths both diagnostic at the genus level and specific to each plant structure (e.g., Mbida Mindzie *et al.* 2001, Lentfer 2009a). Based on a finding of banana phytoliths at a site in Cameroon (Mbida Mindzie *et al.* 2001), it was shown that bananas diffused to Africa from Asia 3,000 years ago. The work also confirmed that agriculture was being practiced in the African rainforest at this time. A large number of more recent studies indicate that *Musa* phytoliths occur in ancient sediments throughout the Old World and will be valuable in tracing the genus' history in Asia, Africa, island southeast Asia, and Oceania (Donohue and Denham 2009, Fuller and Madella 2009, Horrocks *et al.* 2009, Lentfer 2009a).

Musa is a large genus with a diverse array of different sections, species, and subspecies, and human manipulation during prehistory led to different cultivars, hybridization events, and ploidy levels. Discriminating wild and cultivated plants

and different sections of the genus in various regions with phytoliths is a more complex issue than making genus-level identifications, and is a focus of current research (e.g., Lentfer 2009a, Vrydaghs *et al.* 2009).

4 Understanding the biology of phytolith formation and morphology

Of considerable significance for the ability of investigators to effectively study ancient phytoliths is the dramatic increase in understanding of the biology of phytolith formation. For example, active (i.e., purposeful) uptake of silica by plants and the subsequent directed placement of solid silica in specific structures and tissues of plant species has been demonstrated (Piperno 2006a). Going further, research by Ma *et al.* (2006) on rice led to the first identification of a silicon transporter gene in a higher plant. Called *Lsi1*, this genetic locus was shown to control the uptake of soluble silica by plant roots from the ground soil. These findings negate the traditional notion that phytoliths are little more than waste products passively accumulated by plants. Rather, phytoliths are now thought to have three major types of function: structural, physiological, and protective (Sangster *et al.* 2001, Piperno 2006a). The protective functions, whereby plants defend themselves from their herbivores and pathogens by incorporating a hard and indigestible substance like solid silica in their various structures and tissues, appear to play critical roles in silicification patterns and phytolith morphology. This is notably known to be the case in two major crop genera, *Zea* and *Cucurbita* (Dorweiler and Doebley 1997, Piperno *et al.* 2002, Piperno 2006a).

Also importantly, newer taxonomic and phylogenetic information on gymnosperms and angiosperms (e.g. GPWG 2001, Soltis and Soltis 2004) has provided archaeobotanists with valuable insights into the evolution of phytolith formation and morphology. In many cases, there is a strong correspondence between phytolith production/shape/surface ornamentation and a plant's higher- and lower-order taxonomic affiliations, indicating that a shared ancestry in plants resulted in shared production and morphological patterns (Piperno 2006a). The final link in this chain of evidence is the direct demonstration of genetic control, including control by individual Mendelian segregating genes, over phytolith formation and morphology in three major crop plant genera, *Zea*, *Cucurbita*, and *Oryza* (Dorweiler and Doebley 1997, Piperno *et al.* 2002, Zheng *et al.* 2003, Piperno 2006a). Major domestication genes that code for crucial phenotypic changes, such as for naked kernels and soft glumes in maize (the genetic locus called *teosinte glume architecture1*) and soft fruit rinds in squashes (called *hard rind*), also result in transformations in phytolith formation patterns and morphology that allow cultivated maize and squashes to be identified and distinguished from their wild ancestors (see Figure 6.3) (Dorweiler and Doebley 1997, Piperno *et al.* 2002, Piperno 2006a). Interestingly, these genes each control both silicification and lignification, the formation of two major defensive compounds by plants.

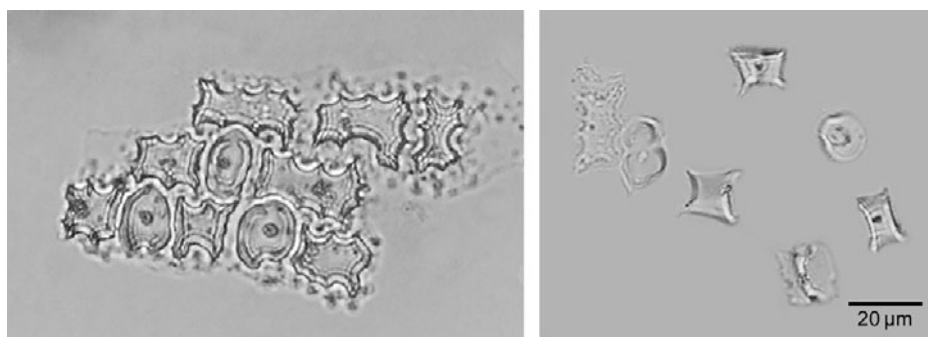


Figure 6.3. Allele *tgal* and phytolith formation and morphology in *Zea*. In teosinte, which carries the *tgal* allele, complete silicification of the epidermis occurs, resulting in phytolith formation in both long and short cells. All phytoliths are highly ornamented with small knobs and projections because they form in juxtapposition to highly lignified cells, which are pitted (left image). These phytoliths identify teosinte presence. *Tgal* is the maize version of the allele. It directs that silicification is largely confined to the short cells, resulting in different kinds of phytoliths that identify maize presence. Short-cell phytoliths are not ornamented as in teosinte because lignin production is also turned off (right image). From Piperno 2006a, copyright AltaMira Press.

In addition to discriminating between wild and domesticated taxa in the archaeological record, it appears that it will be possible to follow the tempo and timing of human selection of some major traits by using these phytoliths. We may expect further direct demonstrations of genetic control over phytolith formation in crop and wild plant taxa.

5 Current starch grain research in archaeobotany

Starch grain studies have recently found archaeobotanical applications as independent indicators of early domestication and agricultural diets in many parts of the world (e.g., Loy 1994, Piperno *et al.* 2000, 2009, Babot 2003, Iriarte *et al.* 2004, Pearsall *et al.* 2004, Perry 2005, Fullagar *et al.* 2006, Perry *et al.*, 2006, 2007, Torrence and Barton 2006, Zarillo and Kooyman 2006, Dickau *et al.* 2007, Pagán 2007, Barton 2008, Messner *et al.*, 2008, Zarillo *et al.* 2008, Boyd and Surette 2010). Botanists and other scholars not concerned with ancient plants have long recognized that different plant species may be identified through the morphological characteristics of the starch grains they produce in their storage organs (seeds, underground structures). Therefore, unlike when the modern period of phytolith research in archaeobotany began during the 1970s, there is a large corpus of literature on starch grain occurrence, morphology, synthesis, and biological properties to which archaeobotanists can refer (e.g., Reichert 1913, Seidemann 1966, Whistler *et al.* 1984, Torrence 2006). This in part accounts for the rapid and geographically widespread “take-off” of the technique.

Archaeological stone tools have thus far been important subjects of research because starch has been found to survive particularly well on ancient stone implements dating from the Late Pleistocene and Holocene that were used to process plants and turn them into foods. These kinds of tools, typically called grinding stones, are commonly found at early sites and they provide robust data for pre-ceramic time periods, when the transition from hunting and gathering to food production began in most regions of the world. In contrast, enzymatic and other processes are expected under many circumstances to quickly destroy starch deposited into sediments; archaeological sediments analyzed thus far have generally conformed to expectations and been found to be depauperate in starch content, although exceptions occur (e.g., Perry *et al.* 2006, Henry *et al.* 2009). Recently, Duncan *et al.* (2009) reported the recovery of a number of different food starches (manioc, potato, arrowroot, *Prosopis*) from the interior residues of 4,200-year-old bottle gourd and squash fruits from a ceremonial area of a coastal Peruvian site. This novel research opens another area of investigation into the documentation of ancient plant foods and social behavior.

It is clear that starch grains are often identifiable at the genus level and that species-specific determinations are sometimes possible. Identification criteria commonly employed are based on grain size, type (simple vs. compound), shape (round, elliptical, polygonal, etc.) and surface features (presence/absence of visible lamellae and other surface ornamentations, position of the hilum) formed as grains develop in their home in plant organelles called amyloplasts. These criteria have constituted the basis for starch grain descriptions and comparisons for many years (e.g., Reichert 1913, Seidemann 1966) and continue to be utilized by many current investigators. Caution should be exercised with the interpretations of a few investigations that have identified starch grains in archaeological sites when the attributes necessary to identification such as the presence of the various distinctive features possessed by starch grains noted above are missing from the particles studied (Horrocks *et al.* 2008). Similarly, descriptions and comparisons of starch grains made simply by automated measurements of shape factors (Wilson *et al.* 2010) are inadequate and not infrequently lead to confusion in classification and identification, including identification overlap between entirely different types of starch, because critical morphological and three-dimensional grain features are not considered.

The construction of modern reference collections for various regional flora is proceeding apace. Extensive study of close wild relatives of crops is necessary to determine whether they can be distinguished from their domesticated products. Research on maize, manioc, chile peppers, *Phaseolus* and *Canavalia* beans, peanuts, squashes, yams, and bananas has begun, showing potential for the discrimination of some, but not all, wild from domesticated species. For example, it appears that wild and domesticated *Zea*, *Manihot*, South American *Cucurbita*, and *Capsicum* can be distinguished (although differentiating among the domesticated chile species may prove to be difficult if sample size is not large), but it will be difficult to discriminate beans of domesticated *Phaseolus* and *Canavalia* and

some yams from wild congeners (Fullagar *et al.* 2006, Piperno 2006c, Holst *et al.* 2007, Perry *et al.* 2007, Piperno and Dillehay 2008, Duncan *et al.* 2009). Studies investigating whether wild and domesticated species of wheat, barley, and rice can be differentiated have not yet been undertaken. Lu *et al.* (2005) noted differences between starches from millets and other cereals. Banana and *Ensete* fruit starches appear to be identifiable at the genus level and below, adding another component to this important line of archaeological work (Lentfer 2009b).

There is little question that starch grain synthesis, essential to a living plant, is under biological control and that many morphological features of a starch grain are inherent characteristics of the individual genus and species that produces it (e.g., Reichert 1913, Seidemann 1966, Whistler *et al.* 1984, Piperno 2006c, Torrence and Barton 2006). Because the domestication process sometimes involved changes in starch grain properties, it would make sense that size and morphological attributes in starch might be under the control of domestication genes involved with various aspects of starch synthesis. A recent study comparing maize and teosinte found that starch grains are consistently larger in maize and that significant morphological differences exist between the two subspecies (Holst *et al.* 2007). This obviously opens another avenue for studying maize domestication in its cradle of origin, important also because pollen does not reliably separate teosinte from maize (Holst *et al.* 2007). Interestingly, genes involved in starch yield and other properties such as “pastiness” (the quality that makes maize suitable for making tortillas) have been identified in maize, and they are thought to have been targets of human selection during domestication and subsequent improvement (Whitt *et al.* 2002). It should be possible, through side-by-side comparisons of detailed genetic data from wild/domesticated maize and starch grain size/morphological attributes in the same specimens, to robustly ascertain what roles genetic factors and individual genes play in determining the attributes that separate maize and teosinte starch.

More basic aspects concerned with carrying out starch grain analysis in archaeobotany are also sure to see extended study in the near future. For example, current research is showing that it is possible to recover starch grains from a wide array of different contexts, including food residues in ceramic pots and the calculus of human teeth (Crowther 2005, Boyadjian *et al.* 2007, Henry and Piperno 2008, Piperno and Dillehay 2008, Zarillo *et al.* 2008). Methodological experimentation to further refine nondestructive ways to remove calculus from teeth, and to recognize and identify grains damaged by cooking that apparently also survive in high numbers on teeth and in ceramics, has been and will continue to be carried out (Piperno and Dillehay 2008, Zarillo *et al.* 2008, Henry *et al.* 2009). Questions to be answered include whether starch from different plant organs such as seeds and underground structures are more/less susceptible to being destroyed when foods are cooked by various methods that would have been used in prehistoric times (e.g., parching, hot rock boiling, pit roasting). It may even be possible to reveal ancient cooking methods through the types of morphological damage present on heat-altered starch grains.

6 A more detailed look at some new archaeobotanical studies from the Neotropics and their implications

It is useful here to consider in more detail two new studies of early agriculture in the Neotropics, one dealing with the diffusion of maize into Ecuador and the other with agricultural emergence on the western slopes of the Andes in Peru. These studies have importance for both older and newer debates on domestication and crop dispersals in the Neotropical forest.

6.1 Early Valdivia agriculture

The question of maize use by the Valdivia cultures of southwestern Ecuador, who were some of the earliest makers of ceramics in the New World, together with the overall nature of Valdivia subsistence – were these people established farmers or not? – has been a subject of discussion and debate since these sedentary villages were discovered in the 1950s. In the late 1970s, Zevallos, Galinat, and Lathrap reported impressions made with maize kernels on Valdivia III ceramics dated to 5,000 years ago (Zevallos *et al.* 1977). They argued from this and other evidence characteristic of Valdivia occupations (e.g., artifact assemblages with numerous manos and metates and spindle whorls for weaving cotton; ceremonial mounds; permanent settlements positioned to exploit rich river bottomlands) that Valdivia was an early expression of established farming with productive maize agriculture; i.e., the beginning of the Formative Period. However, the issue could not be studied in robust archaeobotanical terms because macrobotanical remains were poorly preserved. Beginning in 1978, Pearsall and her students applied a series of phytolith and starch grain analyses to a number of Valdivia occupations, particularly the well-studied one at Real Alto. The large corpus of results from sediments and grinding-stone residues consistently indicated that maize phytoliths and starch were present in contexts radiocarbon-dated to about 5,000 years ago (e.g., Pearsall 2002, Pearsall *et al.* 2003, 2004). Associated with the maize were a number of other crops, such as leren, arrowroot, squash, manioc, and jackbean.

Doubts persisted among some researchers concerning presence of maize and well-developed agricultural systems during early and middle Valdivia times (c. 6,000 to 5,000 BP). Some of these reservations were residues from earlier debates when doubts that the tropical forest could have supported well-established agriculture during that period were common. Some were also by-products of the “maize wars”, the protracted debate that was taking place on the origins and dispersals of maize (see Piperno and Pearsall 1998 for a discussion). Staller and Thompson (2002) mounted a direct challenge to Pearsall’s results, asserting that none of Pearsall’s microfossil data and dates for maize (and by implication for other crops) were valid. They argued that maize did not appear in Ecuador

until about 4,000 BP, basing their case on phytoliths recovered from ceramic vessels from a late Valdivia ceremonial site located in southern Ecuador, La Emerenciana, that was first occupied 4,000 years ago. The age and ceremonial nature of the site actually make it of little relevance to the question of whether maize was present earlier in Ecuador and routinely consumed in domestic contexts, and Staller and Thompson's interpretation of their own phytolith data raised many questions (see Pearsall 2002 and Piperno 2003 for detailed comments on the validity of the arguments).

Zarillo *et al.* (2008) applied microfossil data to the issue one more time, using starch grain analysis in a different way – by recovering and directly dating starch grains from carbonized food residues in early Valdivia ceramics. The samples came from Loma Alta, one of the earliest and best-studied Valdivia village sites, where J. Scott Raymond and his colleagues have carried out investigations for many years. The results indicated that starch grains from cooked foods can survive in an identifiable form in ancient pottery (see discussion in Zarillo *et al.* 2008 that explains why). The pots studied contained numerous starch grains from maize along with crops such as manioc, leren, chile peppers, squash, and jackbean. The residues from three of the pots containing these starch remains were directly radiocarbon-dated and all returned ages of 5,300 BP. Grinding stones from Loma Alta dated by associated charcoal to this time and several hundred years earlier also contained maize starch.

These results are important for a number of reasons. A battery of different starch grain and phytolith studies carried out over the past 30 years – on sediments, stone tool residues, and now ceramic food residues – are uniformly consistent in demonstrating that maize was present and routinely consumed throughout the early and middle Valdivia cultural sequences. Furthermore, views first expressed years ago by Donald Lathrap and others (e.g., Zevallos *et al.* 1977) that tropical forest Valdivia people were well-established and productive farmers who grew and consumed a variety of crops, including maize, are supported by these archaeobotanical data. The study by Zarillo and colleagues opens an additional avenue of dietary investigation that should be widely applicable to ceramic period occupations throughout the world (see Boyd and Surette 2010 for an example from northern North America).

6.2 The Ñanchoc culture

There is an early to middle Holocene pre-ceramic culture called Ñanchoc that is assuming considerable importance in documenting early South American agriculture. Discovered and investigated over the past 30 years by Tom Dillehay and colleagues (e.g., Dillehay *et al.* 1989, 2007), these sites, over 40 in number, are located in northern Peru on the lower western slopes of the Andes in the Zaña Valley (Figures 6.1b, 6.2). Dating to between 11,000 and 6,000 BP, they are small and, after 9,000 BP, permanent occupations along the banks of small streams

at 500 m above sea level in a tropical dry forest setting. Macrobotanical remains of crops such as peanuts, *Cucurbita moschata* squash, manioc, and cotton are preserved. Dillehay *et al.* (2007) recently reported dates directly determined on the peanuts and *C. moschata* of 10,200 and 8,500 BP, respectively.

I recently carried out a starch grain study of the calculus or plaque on human teeth from ten different individuals from the Ñanchoc occupations comprising adult and subadult members of the population (Piperno and Dillehay 2008). The dental specimens were recovered in direct association with the plant and other cultural remains such as human bone that yielded dates of between 9,000 and 7,500 BP. Starch grains commonly occurred on numerous teeth from this time period, and on every tooth more than 70% of them derived from four foods: *Phaseolus* beans, *C. moschata* fruit flesh, peanut nuts, and the fruits of *Inga feuillea*, a tree crop. Two of these taxa, *Phaseolus* and *Inga*, did not occur in the macrobotanical record. The *Phaseolus* grains were much larger than those in modern wild *P. vulgaris*, ruling wild common beans out from representation. However, it could not be conclusively determined whether a domesticated lima and/or common bean was present because there is a good deal of size and morphological overlap between wild *P. lunatus* and domesticated *Phaseolus*, and in all but one sample the Ñanchoc starch attributes fell into this overlap zone. Nevertheless, because the sites are outside of the native habitat of wild *Phaseolus*, the bean starch likely represents cultivated plants.

It thus appears that four cultivated and/or domesticated plants were routinely consumed during the ninth and eighth millennia BP. The starch evidence firmly indicates that early domesticated *Cucurbita* was routinely consumed and not used primarily for utilitarian purposes, such as for net floats or containers. Moreover, the fact that people were eating fruit flesh (the macrobotanical remains were seeds) implies that selection for the major domestication gene that controls for nonbitter flesh in *Cucurbita* had occurred. In a similar regard, it could also conclusively be determined that starch identified as *Phaseolus* derived from the beans, not the pods, of the plant (the starch from each part differs on the basis of morphology; D. Piperno, unpublished data), indicating that cooking techniques were effective in removing the toxic chemicals that raw beans possess in considerable quantities. Presence of numerous cooked grains on the teeth, including some that were still identifiable as *Phaseolus*, further adds to this picture.

The peanut information is also interesting for a number of reasons. The macrobotanical remains derive from the hulls of the nuts and they do not exhibit all the features typical of modern domesticated plants (Dillehay *et al.* 2007). They almost certainly represent cultivars because they occur far outside the natural distribution of the genus in southern South America. The data therefore give evidence of a protracted period of pre-domestication cultivation of this plant. The peanut starch, on the other hand, is a match for modern *Arachis hypogaea* in size and morphology, and different from starch from modern wild peanuts closely related to *A. hypogaea* studied to date (Piperno and Dillehay 2008). Additional work is needed but it seems that these cultivars have a combination of wild and

domesticated-type traits, and thus perhaps the suite of phenotypic attributes that characterize domesticated peanuts did not develop quickly or simultaneously after cultivation began.

It is often difficult to confidently estimate for early periods of food production how many dietary calories were derived from cultivated and/or domesticated vs. collected plants. This has resulted in many questions concerning the trajectory and intensification of food production in the New World, given that large sedentary and nucleated villages conventionally associated with truly effective farming post-date 6,000 BP (see Piperno and Pearsall 1998). Starch grain analysis of dental remains provides a new and direct approach for studying this issue. The starch grain data considered with other evidence from the Nanchoc sites indicates that these people were not casual food producers but rather committed farmers who derived significant dietary inputs from cultivated and domesticated plants. There are other areas of the Neotropics with the same indications. For example, by 7,600 BP in central Panama a variety of domesticated plants were being grown, and paleoecological evidence along with extensive archaeological foot surveys indicates that settlements were common and people were organized as swidden farmers who were systematically cutting and burning significant areas of forest (e.g., Piperno and Pearsall 1998, Piperno *et al.* 2000). Therefore, the appearance of large sedentary and nucleated villages should no longer be considered as the first expression of agriculture in the Americas, but rather a development out of earlier, effective food production systems. These themes are likely to assume greater prominence as our understanding of Early and Early Middle Holocene food production in the Americas increases.

7 Ancient plant DNA in archaeobotany

The potential and limitations for studying another type of microplant remain, DNA, retrieved from archaeological plant macrofossils are becoming better understood, as they are for ancient plants generally. Two recent, major reviews provide an excellent summary and analysis of what has legitimately been achieved in the New and Old Worlds, what can be done at the present time, and what is conceivable in the future (Willerslev and Cooper 2005, Schlumbaum *et al.* 2008). With respect, for example, to the long-term survivability of DNA, current research indicates that noncarbonized remains are much more likely to contain useable DNA than are charred plants, and that waterlogging is frequently but not always destructive of DNA (hard seeds may offer better preservation in these contexts) (Schlumbaum *et al.* 2008). Well-preserved DNA has been recovered from archaeological specimens of Holocene-age sites located in very dry environments, but other studies, including of older DNA from nonarchaeological contexts, indicate that cooler temperatures offer the best conditions for long-term survival (Willerslev and Cooper 2005). Mitochondrial, nuclear, and chloroplast genes have all been studied, providing a diversity of genetic material with which to best

address different genetic questions. Issues surrounding the control of contamination and authentication of results are complex and widely discussed. Willerslev and Cooper (2005) provide an excellent review of these subjects.

Ancient DNA studies have contributed often unique information in archaeobotany in a number of ways, including: (1) identifying plants at levels more precise than possible through conventional analysis of macrofossils, (2) revealing the original geographical source area of plant remains, and (3) following early artificial selection through the documentation of domestication genes in crop specimens. Two prominent papers published recently illustrate some of these issues. Jaenicke-Després *et al.* (2003) were able to analyze three different nuclear genes in maize cobs recovered from Mexico and the southwest USA that were directly dated to 4,400 BP and 2,600 BP, respectively. One of the genes, *sugary 1*, is concerned with starch quality, while the others underlie plant architecture (*teosinte branched 1*) and kernel protein quality (*prolamin binding factor*). The alleles for all three genes in the Mexican samples were matches for those in modern maize, whereas at the *sugary 1* locus, the southwest USA maize still carried the teosinte copy of the allele, which is rare in modern maize. This evidence indicates that not all of the major domestication genes in a crop were transformed from their wild states simultaneously by ancient farmers, and that regional differences sometimes existed as to which traits farmers were most interested in transforming when crops became available to them.

A study by Erickson *et al.* (2005) on the bottle gourd (*Lagenaria siceraria*) using chloroplast DNA showed that the plant was initially introduced to the Americas from Asia, not from Africa as a result of ocean currents as was previously thought. The study indicates that humans first transported the plant across the Bering Straits when they colonized the New World. This research also provided a re-analysis of the earliest New World archaeological specimens, which were directly dated to between 10,000 and 8,000 BP, showing that domestication had occurred by that time. This indicates that the plants that humans initially carried into the New World likely were already domesticated, and that the bottle gourd, therefore, is one of the oldest domesticated plants anywhere.

7.1 Ancient phytolith DNA?

Before archaeobotanists became seriously interested in phytoliths in the 1970s, earlier researchers, who were the foremost botanists of their generations, had contributed a number of important studies dealing with phytolith formation. One pattern documented in grasses was how the nuclei and cytoplasmic contents of the cells were broken down and replaced with a form of soluble silica, which then quickly solidified (e.g., Blackman and Parry 1968). This process causes some of the carbon of the cell to become trapped by the penetrating silica, remaining there immune from post-depositional adulteration for as long as the phytoliths are stable in the sedimentary environment. Sometimes the remains of the cell contents

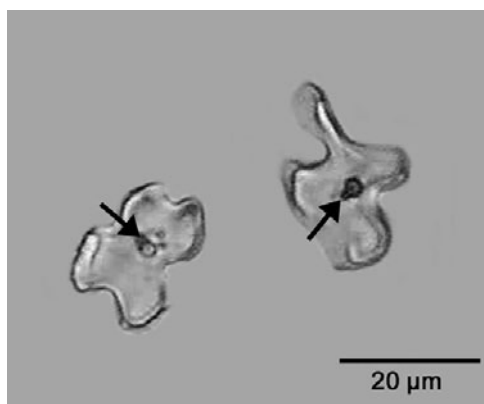


Figure 6.4. Phytoliths with visible carbon inclusions (arrows) from a modern maize leaf. The carbon is a suitable substrate for radiocarbon dating, and its potential for DNA study will be investigated in the future. From Piperno 2006a, copyright AltaMira Press.

are visible as granules or dark spherical cavities, and earlier researchers noted that they might represent specific structures such as nuclei (Frohnmeier 1914, Blackman and Parry 1968) (Figure 6.4).

It has recently been established that the carbon in phytoliths can be directly dated and used for stable carbon isotope study (Piperno 2006a: 125–33). Another area of potential utilization of this carbon is for ancient DNA work. If archaeological phytoliths contain DNA suitable for study, many important questions relating to crop plant origins will be open to another powerful avenue of analysis. The subject is currently in its infancy. A study carried out recently detected no DNA in either phytoliths recovered from an Iron Age site in Israel or a sample of modern wheat phytoliths (Elbaum *et al.* 2009). Preliminary research, on the other hand, by Edward Buckler indicates that DNA was present inside phytoliths retrieved from an archaeological site in Peru (Piperno 2006a). This subject will continue to see exploratory research. It may turn out that some environments are better suited to the preservation of phytolith DNA than others, and that phytoliths from different taxa are for some reason more or less likely to have DNA in quantities allowing analysis. The optimal quantity of different types of phytoliths for investigation must also be established.

8

Conclusions

The accumulated microfossil information and, where possible, its amalgamation with macrofossil results illustrate how a multifaceted set of archaeobotanical data can elucidate long-discussed issues related to the emergence and spread of agriculture. Every method now practiced by archaeobotanists can independently evidence wild plant utilization and domestication, but none of them should act as stand-alone sources. Each has strengths and weaknesses that can be balanced

against the stronger and less compelling aspects of the others. For example, phytoliths and macro-remains often do not increase our understanding of root crop domestication because the former are frequently under-produced in underground organs (with important exceptions such as *Calathea allouia*) and the latter do not survive in humid environments. However, starch grains are beginning to provide the long-sought-for approach to following the history of the many root crops that were domesticated in the New and the Old World (e.g., Piperno *et al.* 2000, Perry 2005, Fullagar *et al.* 2006, Piperno 2006c, Dickau *et al.* 2007).

Another obvious strength of examining all the possible lines of evidence is the power of having more than one independent and strong source of data on any problem. For example, documenting maize dispersals into Panama and Ecuador was made easier by the fact that the plant produces both diagnostic starch and phytoliths in its cobs (phytoliths in the chaff and cupules, and starch in the kernels). These types of microfossils routinely appeared together on the same grinding stones recovered from the same contexts that had also yielded sediment phytolith evidence for maize cob (and leaf) decay (e.g., Piperno *et al.* 2000, Pearsall *et al.* 2003, 2004). The fact that identifiable phytoliths may occur in more than one structure of a plant species not only makes the documentation of that species more robust; it also creates opportunities for examining questions about exactly how the crops were first utilized.

It was recently proposed, for example, that what initially attracted people to teosinte and then maize was not the seeds of the plants for their use as grains but the sugar in their stalks for the production of fermented beverages (Smalley and Blake 2003). Subsequent phytolith research showed that maize and teosinte stalks have identifiable phytoliths that can be used to directly test this hypothesis (Piperno *et al.* 2009), and an analysis of an archaeological site in the Central Balsas region indicated that these phytoliths were absent from early pre-ceramic deposits dated to 8,900 BP, whereas maize starch grains, derived from the kernels, were common (Piperno *et al.* 2009). Thus, the data failed to support the Smalley and Blake hypothesis. How starch grain evidence can also elucidate these kinds of issues has been discussed above for the case of early *Cucurbita* use in Peru.

Molecular studies of modern wild and domesticated taxa have made enormous contributions to agricultural origin studies, and ancient DNA work is established and growing. A considerable amount of basic research is needed to ascertain whether a future growth area in this field will be DNA found in archaeological phytoliths. It is already clear that phytoliths whose formation and morphology have been shown to be under genetic control in *Zea* and *Cucurbita* can provide data on the tempo and timing of human selection on some major domestication genes. Basic research on these topics should follow in starch grain research.

In sum, phytoliths and starch grains are highly versatile fossils capable of providing empirical data on a wide range of issues. We will never have perfect archaeobotanical records but their completeness and accuracy have been, and will continue to be, considerably improved with the incorporation of microfossil methods and data.

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7 How and Why Did Agriculture Spread?

Peter Bellwood

My book *First Farmers* (Bellwood 2005) contains my interpretation of the impact of food production on the world-wide distribution of human variation – archaeological, linguistic and biological – as visible at the regional appearances of historical records and prior to the massive population relocations of the past 500 years. The book contains a central theory about the relationships between increasing dependence upon food production, human demography, and population dispersal with farming cultures and languages in train. In it, I evaluate data from archaeology, linguistics, and genetics as independent lines of evidence focused on three central questions: why did farming societies come into existence in prehistory; where, when, and how did they originate in geographical terms; and by which mechanisms and in which directions, did they spread?

Concerning the latter question, which will be the main focus of this chapter, I infer that increasing dependence on food production led to upward trends in population density, and ultimately to population dispersal as early farmers came to depend more and more upon agriculture and animal husbandry for their subsistence, in a world that was still very much the preserve of lower-density hunter–gatherers and still unravaged by the high-population-density diseases of more recent history. However, agricultural dependence was not necessarily an instant result of agricultural origin, and in some cases the two might have been separated across several millennia in time by a period of pre-domestication cultivation and husbandry, as documented by current research in the Levant and China (see [Chapters 4, 5, and 9](#), this volume).

In addition, I infer that most early Holocene foragers would only have adopted agriculture under favorable demographic, social, and environmental circumstances. Successful shifts into food production by foragers in history or ethnography, such that the erstwhile foragers have since maintained their cultural and linguistic independence, have been rare, particularly in regions such as Australia and much of the western USA that were until recently dominated by hunters and gatherers. Farming in general spread on a much greater scale with farmers, and of

course to foragers who were in direct interaction with farmers, than it spread through unilateral adoption by foragers with no farmer presence in the vicinity.

Unfortunately, archaeology is a discipline poorly situated to pronounce directly on issues of human population dispersal, hence the very high levels of contentious debate that have encircled the theme of “migration” in recent years. Archaeologists recover material culture, evidence of past economies, and the bulk of the world’s ancient skeletal database. But unless they focus on the latter they do not have a direct window on the actual humans, as opposed to their cultural creations. Because of this, the history of the major agriculturalist language families as reconstructed by comparative linguists can be of great significance. This is because one can argue that languages are more closely tied to their biological possessors than are items of material culture and economy. After all, crops, animals, and material goods can be exchanged, as well as carried by migrants, whereas whole languages (as opposed to individual lexical items) are far less likely to travel great distances as whole-population vernaculars through processes of borrowing or shift without native speaker movement (Bellwood 2010).

Given that the major language families of the world had all (if we exclude the Colonial Era) attained their geographical limits before history began, in other words in full prehistory, we can infer from the comparative world-wide archaeological record that the early spreads of language families probably occurred in the mouths of speakers who belonged to relatively small-scale societies, rather than literate conquest empires. This applies to both agriculturalist and hunter–gatherer language families alike. As Ostler (2005) has recently described in detail, the historical empires that existed before AD 1500 had precious little *enduring* impact on the overall distributions of language families, apart from their heavy-handed roles in language extinction. Ancient foundation spreads of language families occurred with actual speaker movements, not through ephemeral military conquest or language shift alone. Therefore, if we are to explain the spread of a major language family on a continental scale, we need to look for a widespread transition within the archaeological record during which considerable population and cultural upheaval could have occurred.

Another observation of great significance is that agriculturalist language family homelands, as identified by linguists from subgrouping criteria, tend to cluster around the zones identified by archaeologists and palaeobotanists as agricultural homelands (Bellwood 2005). The Middle East, China, West Africa, the New Guinea Highlands, and Mesoamerica all present arguable examples of this phenomenon (Figure 7.1), which supports the hypothesis that food production and languages spread together to a high degree. These observations mean that language is equally significant to material culture as an indicator of human history, at least during the recent millennia during which comparative linguists can reconstruct language family internal genealogies. Indeed, the patterning of language families might be the clearest nonbiological evidence available to us for the Holocene history of ancient population movements, of both farmers and foragers alike.

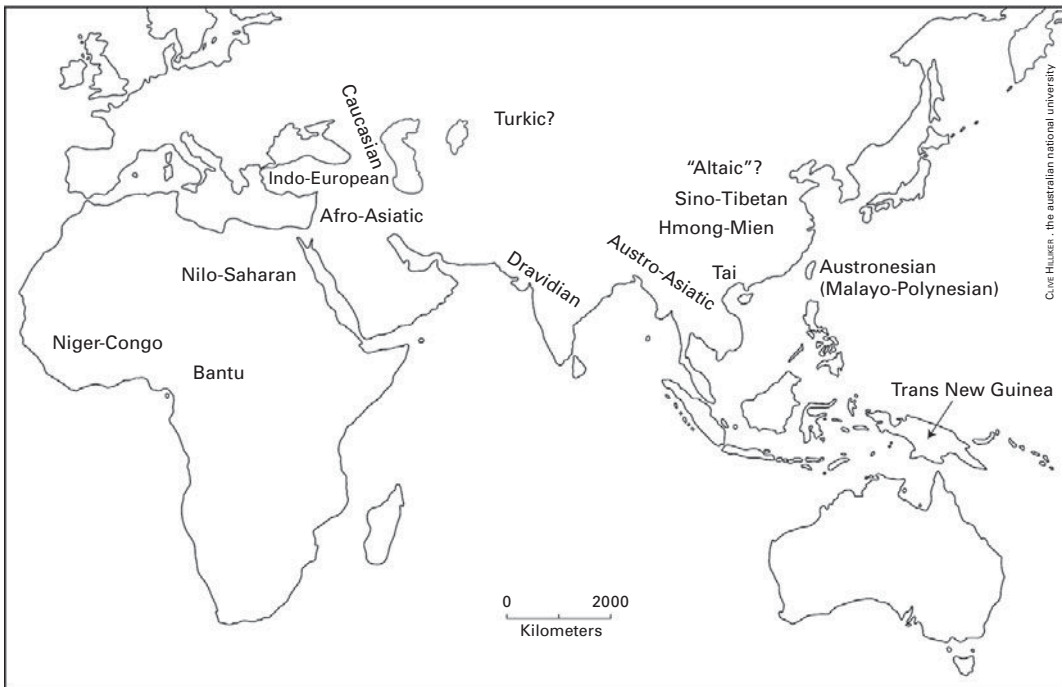


Figure 7.1. Suggested homelands for the major Old World language families, derived from interpretations of the linguistic literature. The Levant with Anatolia, West Africa, central East Asia (“China”), and the New Guinea highlands are all recognized homeland regions for food production. See Bellwood 2005, 2008 for details.

Within human biology, the histories of NRY and mtDNA lineages can serve as useful indicators for the histories of complete human populations, but we still have a long way to go in terms of interpretation of results, especially given current doubts about the accuracy of molecular clock calibrations in recent evolutionary time. All mtDNA and NRY lineages mutated into existence in specific places, but turning each one into a homeland for a human population that lived five, ten, or more (sometimes many more) millennia ago, using data drawn only from modern populations, requires a considerable leap of faith. Subsequent population movements (especially involving adjacent populations who were already closely related genetically, as must have been many early farmers and neighboring populations of foragers), genetic drift, natural selection, and repeated founder effects in small populations surely mean that the haploid genetic profile of a population currently occupying a region will have rather nonspecific links with those of a population in the same region 5,000 or 10,000 years back in time.

However, the remarkable new developments in comparing world populations across the whole genome, using data for up to one million autosomal nucleotide polymorphisms, are now producing exciting new perspectives (e.g., Li *et al.* 2008),

even though clear answers to specific problems of population history such as those addressed here still lie in the future. There is another important source of information from ancient DNA, when it is preserved (rarely in warm climates) in the bones of early farmers and their animals in both putative homelands and regions of immigration. But these developments have so far produced few results relevant to the issues to be discussed.

My operational model for early agriculturalist dispersal is that of “demic diffusion” involving a food producer “wave of advance” incorporating the genes of forager populations, as originally proposed for Europe by Ammerman and Cavalli-Sforza (1979) and more recently clarified for archaeologists by Renfrew (2002). This is a logical mechanism for population expansion, involving continuous population growth in frontier regions, fissioning, and intermarriage with other communities (although to archaeologists the term “diffusion” is often taken to imply movement without any spread of people). The early farming dispersal hypothesis as presented here does not demand extermination of foragers by early farmers, indeed the latter would probably have welcomed new members from foraging communities prior to the development of sufficient population density to promote competition over resources. Furthermore, increasing proportions of “indigenous” genes within admixed and expanding agricultural populations would have been enhanced if the resulting phenotypes carried selective advantages.

The validity of the demic diffusion model is strengthened by analyses of early food-producing cemetery populations that indicate marked increases in birth rate following regional adoptions of agriculture and animal husbandry, but prior to the later increases in mortality due to the more crowded lifestyles that resulted from sedentary life (Bocquet-Appel 2002, Bellwood and Oxenham 2008). Increasing populations must either seek fresh land or intensify production in order to survive, and the former option would often have been inviting in situations fringed by lower-density forager populations. The historical validity of such a model is also revealed for us by a small number of ethnohistorical small-scale and kinship-based tribal populations who managed to avoid the main hazards of the colonial era. One such group were the Iban of Sarawak, swidden rice farmers with long-fallow land requirements who colonized along rivers in small groups before the imposition of colonial government, across a territory stretching over 850 km from western Kalimantan, through Sarawak, to Brunei Bay (Freeman 1970). These movements were encouraged by high population growth (Freeman 1970:132–3) and continued for possibly a century until stopped by the imposition of British rule after 1841.

To an extent, Iban expansion was self-reinforcing. The Iban were an ethnic group well defined by language and identity, who engaged in fairly aggressive territorial expansion through success in warfare, headhunting, agricultural productivity, and the ability to establish new longhouse settlements in areas that previously supported only small populations, often of foragers. According to Freeman (1970:76):

The main incentive behind the remarkable migrations of the Iban has been a desire to exploit new tracts of primeval forest, and the tendency has been for communities to abandon their land as soon as a few lucrative harvests have been reaped, and move on to fresh precincts.

Indeed, achieved male status as a *raja berani* (Freeman 1970:76, Sutlive 1978:27–8) depended on one's possession of the above attributes (and see Bellwood 1996 for founder-focused expansion ideologies in Southeast Asia and Oceania generally). A constant inflow of war captives, who were eventually enfranchised into Iban society, fueled population growth further (Sutlive 1978:31). In a classic sense, the Iban expansion, like that of the ethnographic Yanomami of the upper Orinoco as described by Chagnon (1992; also Bellwood 2005:234), represents a clear case of demic diffusion of food producers into terrain inhabited either by foragers or by other less aggressive food producers.

However, situations such as that of the Iban also indicate to us that biological populations, languages, and cultures need not have evolved through time in absolute unison, simply because one population can absorb another genetically while still maintaining its own linguistic and cultural identity. Austronesians and Indo-Europeans proclaim this very clearly, given the high levels of biological diversity, but language family unity, within both groups. Even so, the components of human variation as expressed through languages and biology do not always have to be completely uncoordinated. Investigating history requires an understanding of how separate disciplinary sources of data can be used in a supportive way – not by circular reasoning, but by understanding how one can compare and combine separate threads of historical “inference to the best explanation” (Foegelin 2007).

1 Inference at the broadest level

The above perspective has many elements that are certainly not new. I acknowledge many stimulating peers and forebears, even if there is not space to list them here (see the list of references in Bellwood 2005). But I believe that Colin Renfrew (e.g., 1992) and I, initially working independently, were the first to apply the hypothesis of early farmer expansion to a *world-wide* canvas from a multidisciplinary perspective, giving where possible equal significance to archaeological, linguistic, and biological viewpoints.

The world-wide results of applying this hypothesis, at least within those latitudes where ancient food production was possible, are presented in Figure 7.1 and Table 7.1. The former shows how language family homelands cluster in and around major food-producing homelands in the Old World: southwestern Asia, central China, northern sub-Saharan Africa, and New Guinea. I have suggested similar correlations for Mesoamerica and eastern North America (early Algonquian, Siouan, and Iroquoian) in Bellwood 2005, and for the Andes, Paul Heggarty and David Beresford-Jones (2010) have an interesting perspective on Chavin expansion and the spread of Quechua. It is impossible to examine all of these situations here,

Table 7.1. Likely origin regions and archaeological correlations for the initial spreads of major language families associated with food production

Language family	Likely region of origin (from linguistic comparison)	Episodes and dates of correlative archaeological dispersal
Indo-European	Eastern or central Anatolia	Western Anatolia to Thrace (and Black Sea?) 7000/6500 BC To Balkans 6300 BC Northern Mediterranean 6200 BC To France (LBK) 5400 to 5000 BC To Denmark and UK 4000 BC Neolithic/Chalcolithic expansion via Iran into Xinjiang and Peninsular India (Tocharian and Indo-Iranian) between 6000 and 3500 BC (see text)
Dravidian	Lower Indus, Gujarat, or central Peninsular India	Contemporary with Indo-Iranian in NW South Asia and triggered by the same background conditions, thus after 3500 BC from Gujarat to Karnataka. Excluded from Ganges Basin by prior presences of IE and Munda (Austroasiatic) speakers
Afro-Asiatic	Levant	PPNB expansion in Levant from 8000 BC, but to North Africa (caprines, Egyptian Neolithic) only after 7000 BC. (No cultural movement from Africa into the Levant is attested during the early Holocene.)
Nilo-Saharan	Sahara/Sahel zone, during wetter early Holocene conditions	Spread of pottery and cattle management commencing <i>c.</i> 8500 BC?
Bantu (subgroup of Niger-Congo)	Cameroon	Eastern Bantu spread with agriculture (and later with iron) between 1000 BC and AD 500
Sino-Tibetan	North-central China (Huang He basin)	6000 BC establishment of millet farming in Huang He basin, but spread of farming into Tibeto- Burman regions not attested until after 3000 BC
Hmong-Mien	Middle Yangzi	Pre-domestication cultivation of rice 6000 BC, but HM linguistic spread is much younger owing to circumscription
“Altaic”	Manchuria, Inner Mongolia, eastern steppes	Probable contemporary with Huang He developments – millet farming by 6000 BC, but dispersal mainly with pastoralism, especially for Turkic speakers
Tai	Guangxi/Guangdong/ northern Vietnam	Origins with agricultural establishment in southern China and northern

Table 7.1. (*cont.*)

Language family	Likely region of origin (from linguistic comparison)	Episodes and dates of correlative archaeological dispersal
		Vietnam, prior to second millennium BC, but most spread (especially into Thailand) much younger owing to homeland circumscription by Austroasiatic speakers located to the south
Austronesian	Taiwan	Taiwan Neolithic standstill 3500 to 2200 BC (see text), then dispersal (Malayo-Polynesian) in two rapid stages: (a) Batanes to Samoa, second millennium BC (b) eastern Polynesia, AD 800 to 1200
Austro-Asiatic	Assam-Yunnan? Ganges Basin? Southern China?	Spread of agricultural societies through Mainland Southeast and Ganges Basin commences c. 3000 BC
Trans New Guinea	New Guinea Eastern Highlands	Spread of systematic agriculture with swamp drainage prior to third millennium BC
Uto-Aztecan	Valley of Mexico/central Mexico	Maize domestication by 4000 BC but spread to US Southwest during second millennium BC (see text). Agriculture lost in Great Basin, and probably adopted by non-UA speaking groups in Mogollon highlands
Otomanguean, Mayan, Mixe-Zoque	Mesoamerica (all circumscribed by the presences of each other, as well as by Uto-Aztecan to the north)	Most agricultural establishment is from 2000 BC, but some early agricultural activity from 4000 BC.
Arawak	NW Amazonia?	Spread of agriculture into Amazonia unlikely to pre-date 2000 BC
Siouan, Iroquoian, Algonquian	Eastern Woodlands – Ohio, Missouri, and middle Mississippi basins?	Native seed crop agriculture by third millennium BC, but farming rejuvenated by dominance of maize after AD 500–1000

but readers should note that I place language families as the main organizing elements in the left-hand column of [Table 7.1](#). This is because most language families are clear and unargued taxonomic entities, with internal subgroup relationships that can be expressed genealogically, unbroken trans-generational transmission, and attached populations of speakers. One cannot structure the human past so clearly on the basis of archaeological cultures or haploid DNA lineages.

2 Three case studies

I have chosen to discuss the Austronesians, the Uto-Aztecs, and the eastern Indo-Europeans (Tocharians, Indo-Iranians, Indo-Aryans), because each of them can be argued to have represented the first food-producing populations in *most*, but not all, of their ultimate areas of distribution. All three have histories of rather contentious debate that have served to obscure what seem like simple answers from a comparative and multidisciplinary perspective. Archaeologists often reject what they regard as simple answers since the past is believed to have been complicated and there is often a philosophical tendency to emphasize the local at the expense of the regional in terms of perspective. I personally have little sympathy for this kind of particularistic, noncomparative approach, and prefer to make inferences from a comparative view of the whole forest as well as an inspection of the individual trees. As David Harris (2008) points out:

...the two approaches, one emphasizing the value of detailed local investigations and the other the need for worldwide comparisons are (in my view) interdependent and equally valid. Nor does the comparative approach imply a commitment to a single ‘universalist’ explanation – only that continental and worldwide comparisons are needed if we are ever fully to comprehend the multiple subsistence pathways followed by human groups as they increasingly intervened in the life cycles of plants and animals through cultivation, taming and domestication.

2.1 The Austronesian dispersal from Taiwan into Central Oceania, 2200 to 1000 BC.¹

The Austronesian-speaking populations formed the most widespread ethnolinguistic group in the world prior to AD 1500 (Figure 7.2). However, despite the clarity of their shared ancestry in a linguistic sense, their biological origins were more diverse (Cox 2008, Friedlaender *et al.* 2008, Hunley *et al.* 2008). Not all Austronesians share a recent genetic origin, and the prehistories of some regions in the western Pacific have involved localized instances of language shift (Blust 2009, Bellwood *et al.* 2011). Nevertheless, it is possible to argue that initial Austronesian migrants spread a food-producing economy, after 2000 BC, throughout Island Southeast Asia and Oceania, with the exception of the interior equatorial highlands of New Guinea, where food production based on tubers and fruits had independent and earlier origins (Denham *et al.* 2004).

Modern comparative linguistic research, based on the identification of uniquely shared innovations to reconstruct a phylogeny of the major Austronesian subgroups, now points solidly to Taiwan as the location of Proto-Austronesian, with the Pre-Austronesian background located in southern China (Blust 2009). A computational analysis of vocabulary items across 77 Austronesian languages has given similar conclusions (Gray and Jordan 2000). As Malcolm Ross notes (in Bellwood *et al.* 2011):

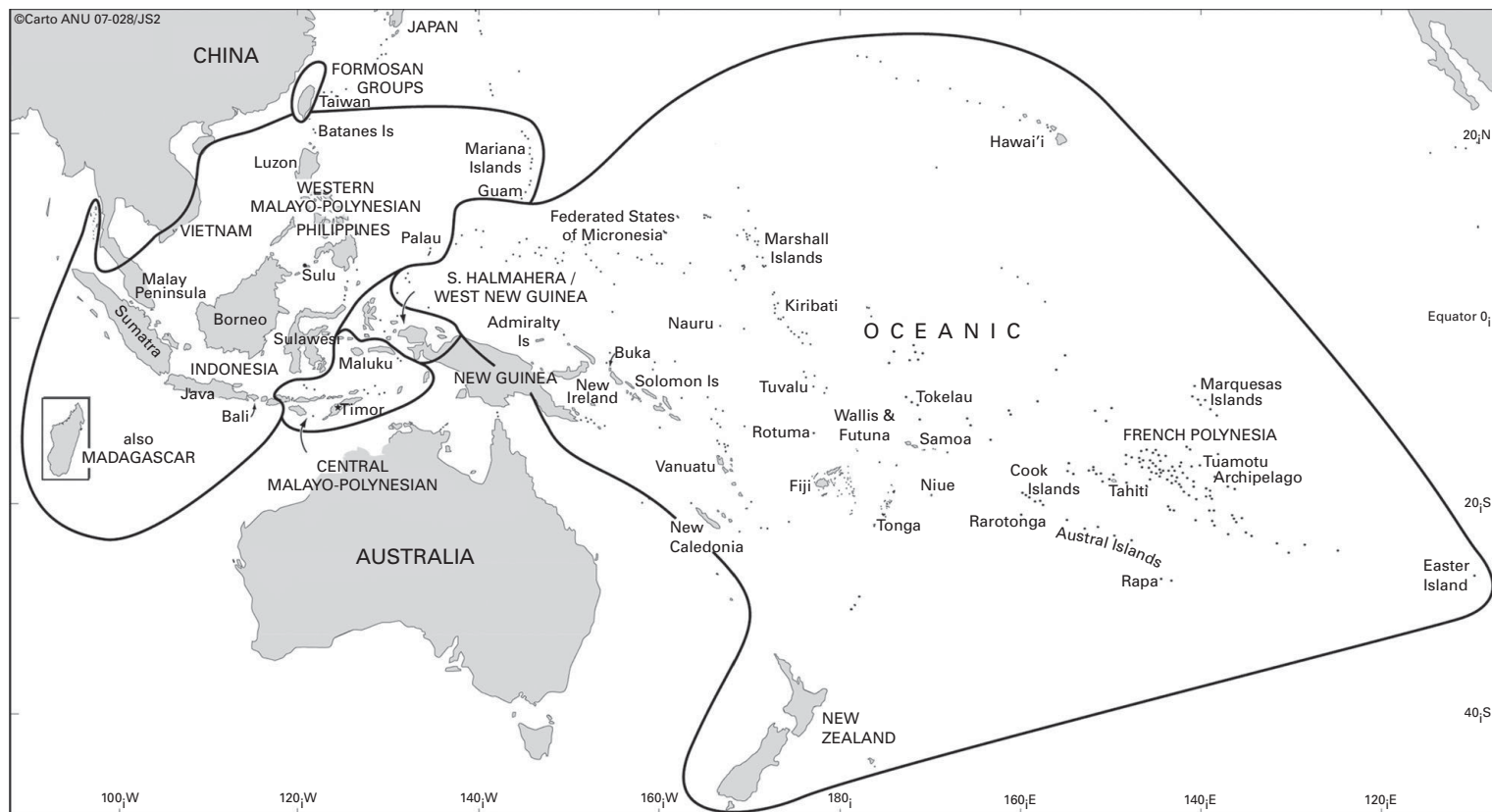


Figure 7.2. The Austronesian language family and major Austronesian language groups.

Eastern Taiwan	Early Neolithic		Middle Neolithic			Late Neolithic		
	Dabenkeng		Fushan			Beinan		
	Coarse cord marked, incised and red slipped pottery		Fine cord marked and red slipped pottery		Red slipped and plain pottery	Plain pottery with rare circle stamping		
	3500 BC	3000 BC	2500 BC	2000 BC	1500 BC	1000 BC	500 BC	AD 1
			Batanes Islands					
			Fine cord marked and red slipped pottery		Red slipped and plain pottery	Red slipped and circle stamped pottery		
			2200 BC?		1500 BC			
			Northern Luzon					
				Red slipped and plain pottery		Red slipped and punctate stamped pottery		
				2000 BC	1500 BC			
								AD 1

Figure 7.3. The linkages between Neolithic assemblages in Taiwan and the northern Philippines.

Of the disciplines represented... linguistics is probably the closest to unanimity about Austronesian origins. All Austronesian languages spoken outside Taiwan belong to a single subgroup, dubbed Malayo-Polynesian by Blust (1977), whilst the thirteen Austronesian languages still spoken in Taiwan belong to several primary subgroups (Blust (1999) proposes nine, on phonological grounds). The logical inference is that Proto-Austronesian was spoken in Taiwan, that it split initially into dialects, and that these dialects eventually diversified into separate languages. Speakers of just one of the dialects, Proto-Malayo-Polynesian, left Taiwan and settled initially either on Lanyu (Orchid) Island, or somewhere in the Batanes Islands, or on the north coast of Luzon. It is speakers of languages descended from Proto-Malayo-Polynesian who have settled the huge expanse of the Austronesian speaking region beyond Taiwan.

Archaeology has recently seen detailed research programs in southern Taiwan, the Batanes Islands, and northern Luzon, with results analyzed in detail by Hung (2005, 2008) and Bellwood and Dizon (2005, 2008). Four factors render a southwards movement of Neolithic material culture from Taiwan into the northern Philippines at about 2000 BC a virtual certainty:

1. The strong parallels in material culture between 2200 and 1500 BC linking southern Taiwan and the northern Philippines, reinforced by the movement of artifacts of Taiwan slate and positively sourced Taiwan nephrite (Hung *et al.* 2007). The synchronous changes in pottery decoration that link SE Taiwan, the Batanes Islands, and Luzon, from a predominance of cord marking through a dominance of red-slipped pottery into a later phase of stamped pottery, are shown in Figure 7.3.
2. The chronological priority in Taiwan of the artifact types concerned, involving an unbroken continuity since at least 3000 BC in cord-marked and red-slipped

pottery, spindle whorls, stone bark-cloth beaters, perforated slate points, notched net sinkers, and adzes and ornaments of Taiwan nephrite (Hung 2004, Hung *et al.* 2007). To these can be added the oldest radiocarbon dates for rice and millet in Southeast Asia (Tsang 2005).

3. The absence of closely related material culture before this time span in nearby regions such as Indonesia or Vietnam.
4. The absence of a prior population in the Batanes Islands. This implies a movement of people to establish a colonization, not an adoption of Neolithic material culture by an indigenous hunter-gatherer population (as probably happened to a degree in the Peñablanca Caves in Luzon – Mijares 2006).

Current genetic evidence (Chambers, in Bellwood *et al.* 2011) supports but does not demand an Out-of-Taiwan hypothesis for the movements of early Austronesians, although recent developments in autosomal genetics (Friedlaender *et al.* 2008) seem to have tipped the balance in favor of southern China and Taiwan. Contrary hypotheses based on mtDNA that favor other regions of Island Southeast Asia depend upon molecular-clock calculations with large and contested error ranges (Hill *et al.* 2007).

In conclusion, with respect to the Austronesians, it is possible to focus on Taiwan and the Philippines at the end of the third millennium BC in order to identify the start of a migration, by both land and sea, of speakers of Austronesian languages and of carriers of a variety of “Neolithic” material culture and food production. Both of these spreads are likely to have been two sides of one “event”, involving a single ethnolinguistic and genetic population in the final resort, albeit one that was constantly adapting and interacting. The migration encompassed warm temperate through equatorial latitudes in the northern hemisphere, and out again in the southern hemisphere, thus passing through some major zones of environmental and resource difference, as well as through pre-existing populations with their own long-established cultures and languages, particularly in western Oceania. One of the results of this equatorial transition appears to have been an abandonment of cereal (rice and millet) cultivation in Indonesia, in favor of the fruit- and tuber-based plant economy that characterized the Pacific Islands.

Why did the Austronesian dispersal occur? Within eastern Taiwan, the archaeological record indicates a marked increase in the number of archaeological sites after 2500 BC (Hung 2008), so population growth and a need for new cultivation land come to mind, given that southeastern Taiwan is a rugged area with low agricultural potential. But early Austronesians moved on to settle new islands very rapidly in terms of both archaeology and comparative linguistics (Pawley 1999). For instance, colonists spread 8,000 km from the Batanes Islands to Samoa in less than 1,000 years. This surely reflected a reliance on *both* maritime *and* lowland agricultural resources, the latter greatly reduced in extent by the drowning of the most fertile alluvial and coastal soils after the sea attained its maximum mid-Holocene level (Bellwood *et al.* 2008). This would have rendered good coastal and

alluvial farmland scarce, creating deep estuaries and steep coastlines against rugged island interiors, at least until clearance-induced soil aggradation began to build up fertile lowlands.

Maritime technology also fueled the Austronesian spread, with the earliest evidence for canoes and paddles in this region coming from coastal central China during the early Holocene. As discussed above, a founder-focused ideology of expansion doubtless helped, but this should have been an effect of maritime migration rather than an initial cause, growing in importance as knowledge of successful colonizations built up in folk memory. Increased frequencies of ENSO climatic cycles perhaps helped to carry Oceanic settlers eastwards (Anderson *et al.* 2006), but this phenomenon alone can hardly explain agricultural or boat-building origins in southern China in the first instance. We are left with a hypothesis that a prior existence of food production, combined with a need for land during a period of population growth and unprecedented coastal drowning, together with an existing boat technology derived from coastal China, encouraged an exodus of the eastern Taiwan population at about 2200 BC. They headed south, and their mostly (but not entirely) agriculturalist descendants continued to head in various directions for the ensuing 3,500 years, ultimately reaching New Zealand by about AD 1200.

2.2 Uto-Aztecan language and maize dispersal from central Mexico into the US Southwest, c. 2000 BC

Past views on the spreads of maize and Uto-Aztecan languages have been derived mainly from archaeology and linguistics, with genetics playing only a minor role (but see below). I summarized the state of play up to 2005 in *First Farmers* (pp. 168–74 for archaeology; 240–4 for linguistics), but I would note, with Steven LeBlanc (2008), that new and exciting developments in both these disciplines have occurred more recently. Within linguistics, the meticulous comparative subgrouping reconstructions by Jane Hill (2001, 2002, 2006, 2007, in press) indicate that early Uto-Aztecan speakers were maize farmers, in contact with early Otomanguean speakers in central Mexico, and that the earliest phases of subgroup differentiation occurred amongst Southern Uto-Aztecan languages rather than Northern. This implies that the language family originated in Mesoamerica rather than the Southwestern USA, and thus refutes older opinions, based on lexicostatistics, of a northerly hunter–gatherer origin amongst Southwestern Archaic hunter–gatherer populations (Hill 2007). Parallel to these linguistic developments, recent rescue archaeology in the Tucson region has revealed settlements of maize farmers with irrigation canals, storage pits, and simple pottery dating from 2000/1500 BC onwards. Excavations of terraced hilltop sites in northern Mexico provide additional support to this emerging new picture, allowing questioning of the older view that maize only spread into the Southwest via forager adoption.

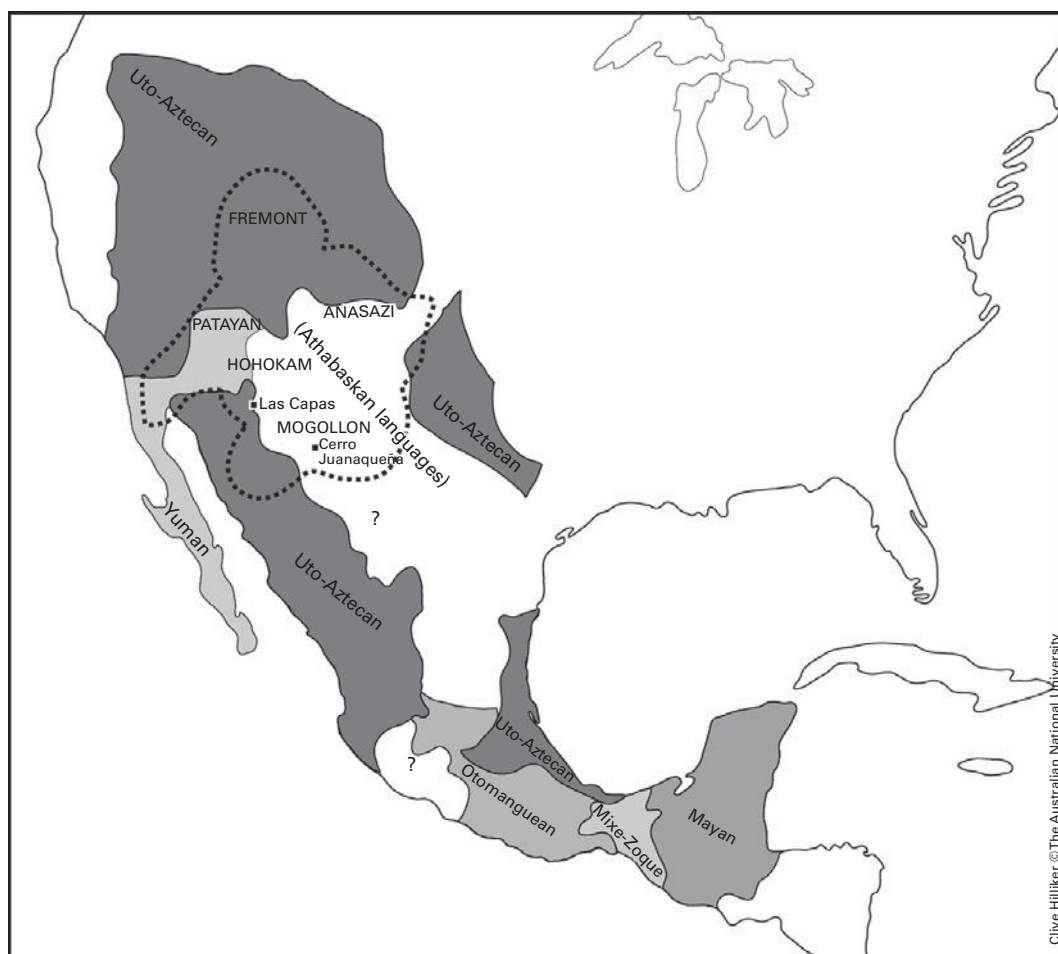


Figure 7.4. The surviving distribution of the Uto-Aztecan language family and its closest neighbors (Athabaskan languages are late prehistoric introductions from the north). Also shown are the distributions of Southwestern cultural complexes with maize cultivation at about AD 1000, together with selected sites mentioned in the text.

My linguistic position on this, as stated above, is that the Uto-Aztecan languages could not possibly have spread over such a vast area, from Mexico, through the Southwest, on to the Plains (Comanche) and as far north as Idaho (Figure 7.4), unless they were carried by existing speakers. Archaeologically, this population can best be identified *initially* (but certainly not always) with maize farmers spreading in search of alluvial farmlands through the semi-desert terrains of northern Mexico and southern Arizona. Some eventually found cultivable alluvial land in quantity in the tributaries of the Gila river in southern Arizona, and it is these people who have recently come to light through the archaeological record. Their descendants continued further, spreading maize farming and mixing to varying degrees with indigenous foragers to become the Anasazi, Mogollon,

and Fremont peoples of Southwestern archaeologists (Matson 2002). Eventually, many of them switched into resource-managing (but not food-producing) wild-plant-based economies in the dry regions of eastern California, the Great Basin, and the Plains.

The archaeological focus here is on the Early Agricultural Phase in southern Arizona, with its San Pedro (*c.* 1300 to 500 BC) and Cienega (500 BC to AD 1) phases. Indeed, new results from the Congress Street Locus in Tucson (Rio Nuevo Archaeology Project) apparently push back the appearances of pit-houses, storage pits, maize cobs, Cortaro bifaces (Mabry *et al.* 2008:164–5), incised sherds, and clay figurines to about 2100 BC, with irrigation canals appearing by 1500 BC (Diehl and Mabry 2006). Whether or not these earliest farmers *depended* on maize for their subsistence is not so clear, and much will depend on how one defines *dependence*, but the crop appears to have become a staple, ubiquitous in the archaeological record, by at least 1300 BC at Cerro Juanaqueña in northern Chihuahua, where it supported an 8 ha terraced hilltop settlement with storage pits and an economy that involved maize and perhaps amaranth production in the valley bottom below (Hard and Roney 2007). At a similar time, the 3.6 ha San Pedro phase settlement at Las Capas near Tucson was supported by 11 ha of irrigated fields and two canals each 1.1 km long (Mabry 2002, Diehl 2005b).

As Huckell *et al.* (2002) have pointed out for SE Arizona, low-level food production (Smith 2001) without irrigation in such a dry environment would have been unviable. This is an extremely important observation that militates against casual hunter–gatherer adoption of maize farming, and Huckell *et al.* emphasize the significance of irrigation for growing maize ears that measured at this time up to 8.4 cm long and 2.9 cm in diameter, and that were stored in pits capable in some sites of holding up to 10,000 cobs – sufficient to feed several people for a whole year. Contemporary rapid stream aggradation in southern Arizona also suggests human impact through tillage and vegetation clearance, although the recent tendency amongst Southwestern archaeologists has been to relate this to autonomous climate change (Mabry 2005). Overall, the data suggest a rapid spread of maize across the Southwest, reaching the Four Corners region by 2000 BC (Mabry 2005, Coltrain *et al.* 2006) and the Rio Grande basin by 1400 BC (Vierra and Ford 2006).

However, as with all good ideas, there are many who do not agree that these early farmers lived in sedentary settlements supported by intensive maize farming (e.g., Mabry 2005, Diehl 2005b, Diehl and Waters 2006, Doolittle and Mabry 2006, Mabry *et al.* 2008). The reasons for this seem to be as follows:

1. Indigenous hunter–gatherers are assumed by the above-listed authors to have adopted maize cultivation.
2. The sites are claimed to contain noncontemporary occupation units such as pits and house floors, indicating mobile and small populations of people engaged in low-level food production, rather than large sedentary village populations.
3. The storage pits are claimed to have been inefficient for maize storage, until large pottery vessels came into use during Hohokam times, after AD 150.

4. The corn cobs are still relatively small (Diehl 2005a, Mabry and Doolittle 2008).
5. People still exploited large quantities of wild resources, more than in later Basketmaker and Hohokam times.

With debates such as this, archaeologists will inevitably place themselves along a continuum of opinion, favoring explanations between low-level food production at one end as opposed to serious dependence on irrigated maize at the other, and the data themselves will be malleable in terms of interpretation. In my view, even if food production in the Early Agricultural Phase in the Southwest at 2000 BC was associated with undeveloped storage technology, small maize cob size, and lack of full sedentism (although I personally doubt all of this), the question still remains – can it have been associated with a spread of food producers from Mesoamerica, or not? Are diet breadth issues and relatively small cob sizes really so relevant if we are testing the ability of food production to fuel population dispersal? The ubiquity of corn in many sites and the associated irrigation and pit storage technologies are sufficient to convince me that substantial food production occurred – even the Iron Age British utilized pit storage, and managed to reproduce enough people to make life slightly difficult for the invading Romans, at least for a while.

Unfortunately, as LeBlanc (2008) discusses, there is little genetic evidence that can adjudicate the migration issue. Malhi *et al.* (2003) have identified a small amount of male migration into the Southwest from Mesoamerica from Y chromosome data, and Hill (2006) notes that men were generally responsible for agricultural activities in ethnographic Uto-Aztecan societies, so perhaps the early farmers often took wives from indigenous forager communities. Recent identification of ancient mtDNA from saliva in preserved chewed quids and blood on women's aprons suggest possible movement of mtDNA lineage A from Mesoamerica into the Southwest (LeBlanc *et al.* 2007). Given the recency of human settlement of the Americas, however, and the relative lack of genetic diversity amongst the founders compared to Old World populations, it will perhaps always be difficult to differentiate New World populations in terms of their genetic origins. As LeBlanc (2008) notes, any early farmers who might have moved from Mexico into Arizona are likely to have been closely related already in genetic terms to resident forager populations. This will mean that not only "farmer" genes will have traveled, but also widely shared "forager" ones as well. Like will have mingled with like, and the "forager" genes would probably not be recognized as having spread at all. This will reduce the visibility of any farmer contribution, which will only be visible through haplogroups actually identified as intrusive by geneticists.

As made clear, I favor an explanation that maize farming and Uto-Aztecan languages spread together with human carriers from Mesoamerica into the Southwest at about 2000/2500 BC (Figure 7.4). If this view is correct, then why did the spread of food production occur? The most likely reason appears to me to be

related to demographic growth, connected with population movement through the difficult semi-desert Sierra Madre foothills of northern Mexico, in which individual foundations of new settlements could have involved crossing considerable geographical distances in search of water and good land. Movement southeastwards into more favorable regions of Mexico would have been constrained by the existing presence of Otomanguean-speaking maize farmers, so it was perhaps northwards or nothing for the Uto-Aztecs.

However, the whole Uto-Aztec expansion was certainly not based on maize agriculture alone. After the short-lived Fremont expansion into Utah, with maize cultivation dated between AD 600 and 1300, some of the northern Uto-Aztecs appear to have settled down to a foraging lifestyle in water-stressed landscapes, while retaining many resource management traces of a deeper food-producing past (Hill 2002). Furthermore, some of the so-called “Eastern Basketmakers” of the Mogollon highlands in New Mexico and southern Colorado are considered to have been indigenous foragers who adopted farming from incoming (presumably Uto-Aztec-speaking) agricultural populations to their west and southwest (Matson 2002, LeBlanc 2008, LeBlanc *et al.* 2008). However, these later adjustments do not overturn the basic model of initial farmer spread.

2.3 The spread of food-producing populations from western Asia into northern India before 3500 BC

South Asia presents a very interesting arena for the spread of food production. Dorian Fuller (2006, 2007) has recently made a case for mid-Holocene independent domestications of *indica* rice in the Ganges Basin, and of native small millets and legumes in Saurashtra and the southern Deccan. However, archaeological evidence associated with these developments is slight, and if they did occur, they seem not to have led to any significant demographic or cultural change among the Mesolithic communities who occupied India down to about 3500/3000 BC. After this date, the Ganges Basin was extensively settled by village-dwelling and copper-using agriculturalists of westerly origin, mixing in the downstream eastern portion of the basin with rice agriculturalists who appear to have preceded them there by less than a millennium. Pastoral and agricultural societies also first appeared in southern India at this time.

A likely explanation for all of this, focused on food-producer expansions, was discussed in *First Farmers* (Bellwood 2005) and elsewhere (Bellwood 2006, 2007–2008). It is possible now to make some very interesting new observations, developing further an argument for Neolithic and Indo-European (IE) language colonization of Pakistan and northern India made persuasively by Colin Renfrew (1987: see his chapter 8, Hypothesis A), but later rejected by him (Renfrew 1999) in favor of his Bronze Age elite dominance Hypothesis B, which followed a more widely accepted model of a much later IE migration eastwards along the steppes north of the Black and Caspian Seas, and then southwards through the deserts

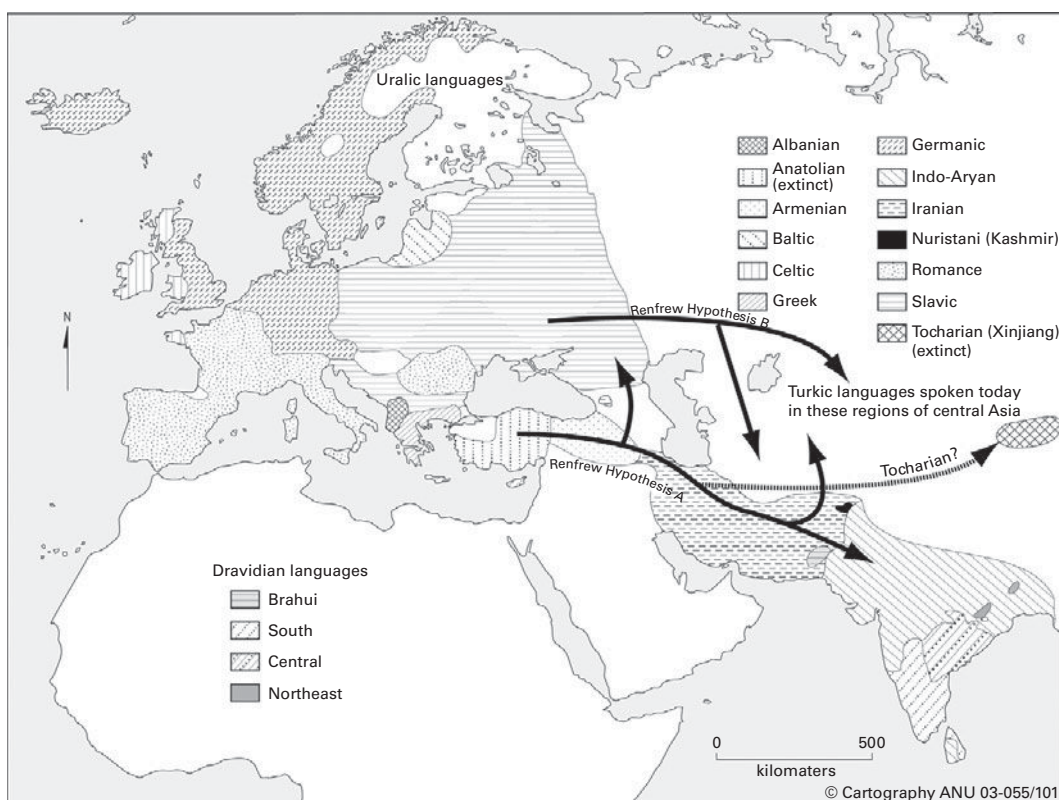


Figure 7.5. The distributions of Indo-European and Dravidian languages prior to the colonial era (except for the extinct Anatolian and Tocharian). Subgroup boundaries after Ruhlen 1987. Colin Renfrew's (1987:Fig. 8.4) Hypotheses A and B for the movements of early Indo-Iranian-speaking populations are shown. Hypothesis A (the more southerly route) is the one favored in this chapter.

and oases of central Asia into Iran and Pakistan (Figure 7.5). Renfrew's original "Hypothesis A", of conjoined Neolithic and Indo-European language migration from Anatolia via Armenia and Iran into Pakistan, entirely south of the Black and Caspian Seas, was in my view correct.

One of the historical documents that has often been brought forward as a witness for Indo-European invasion from the northwest is the compilation of hymns and supplicatory chants known as the *Rigveda*, an oral creation of the middle or late second millennium BC, committed to writing in the late first millennium BC. Parts of the *Rigveda* describe battles and attacks on cities in the region of Punjab, and many earlier authorities regarded this compilation as a record of the conquest, by incoming Indo-Aryan-speaking pastoralists, of a Dravidian-speaking Harappan (Indus Valley) civilization already in decline. The discovery of apparent massacres at Mohenjo-Daro once appeared to support the idea, but current radiocarbon dates indicate that the Mature Indus Phase in

the Pakistan “heartland” had ended by 1900 BC, long before the events described in the Rigveda took place. So perhaps the Rigveda was recording events in a Punjab that was already Indo-Aryan speaking. Furthermore, most of the Mature Harappan sites beyond the Ghaggar River in India were not abandoned, but continued in occupation without a break.

Despite this, many linguists and archaeologists who are tied to a late date for Indo-Iranian linguistic dispersal, from a homeland in the eastern European and Asian steppes, still insist that IE languages could not have entered the subcontinent very long before the period of the Rigveda. Such opinions have been published recently by Witzel (2003), who favors a northern Kazakhstan homeland, and by Anthony (2007) and Parpola (2008), who favor origins further west in the Ukraine. Yet no one has ever been able to point to a significant external cultural intrusion in the archaeology of Punjab or Gangetic India during the relevant time period of 1500 to 1000 BC, even though the Rigveda itself makes a presence of IE speakers in Haryana (upper Ganges/Yamuna basin) at this time indisputable. In seeming frustration, some have argued that either the whole IE language family originated in South Asia (see Witzel 2001 for a powerful demolition of this view), or the IE languages simply floated in without speakers, marching along for unstated reasons through language shift.

My response to all of this in 2005 was to push everything back by 2,000 years, in line with propositions for a much older origin of the IE languages in Neolithic Anatolia at *c.* 7000 BC (Renfrew 1987, 1999, Gray and Atkinson 2003), and in line with the increasingly obvious continuity of northern Indian archaeology from the Early Harappan cultures of *c.* 3500/3000 BC in the northwest, into the early historical period represented by Painted Gray Ware, Northern Black Polished Ware, and the early urban civilizations of the Ganges Basin in the first millennium BC. This moved the IE arrival back into the Chalcolithic (since people used copper in this region at this time), and set it in theoretical perspective as an agricultural colonization of a region that mainly supported hunter-gatherer populations beforehand, who used Mesolithic backed stone tools and who exploited wild plants and animals.

Dravidian-speaking populations spread as pastoralists and farmers through southern India at the same time, perhaps from a homeland in Gujarat or the southern Indus region. However, the Ganges Basin itself has never supported extensive Dravidian-speaking populations, and at 2000 BC the only other well-attested populations in this region, apart from the Indo-Europeans themselves, would have been ancestral Munda speakers. These could well have descended from Austro-Asiatic-speaking rice farmers who spread into the lower Ganges Basin before IE arrival, moving in from Southeast Asia or Assam with cord-marked pottery around 3000 BC, but this issue is not examined here (Fuller 2007 has recently suggested they were indigenous to northern India). The spotlight instead is on the earliest IE speakers (Indo-Aryan languages), whose linguistic descendants today form the vast majority of northern India's population.

Since *First Farmers* was published in 2005, there has been a rapid growth in the archaeological record in the upper Ganges Basin, particularly concerning the Early and Mature Harappan phases in Haryana, Rajasthan, and Gujarat. Many sites here are known to contain the same kind of red pottery with simple black or white painted designs that characterized the Early Harappan in the Indus region itself, where the Hakra Phase dates back to about 3700 BC (Kenoyer 2006). In Haryana, between the former (now dry) Ghaggar tributary of the Indus and the Yamuna River, no fewer than 350 Harappan sites are now reported (Shinde *et al.* 2008). Many, like Girawad and Farmana, have Early Harappan basal layers that contain copper and gold artifacts, as well as painted and incised pottery related to that of the Hakra Phase in the Indus Valley itself. In addition, the post-Harappan cultures of the upper and middle Ganges Basin, especially the Ochre Colored and Black and Red Ware complexes, have clear Early and/or Mature Harappan antecedents (Chakrabarti *et al.* 2004–2005, Bellwood 2005:91–6). Indeed, sites related to the Hakra Phase of the Early Harappan reach virtually as far east as Delhi, and can be identified as the foundations beneath a great deal of the agricultural archaeology of the upper and middle Ganges Basin from 3000 BC onwards.

The implications of this are a bidirectional agricultural settlement of the Ganges Basin, with wheat, barley, sheep and goats moving in from the Middle East via Iran and the Indus region, and rice coming either from eastern Asia or representing a local Gangetic *indica* domestication (at present, *japonica* pre-domestication cultivation in central China pre-dates any parallel evidence in India by over 4,000 years). South Asia itself doubtless witnessed some internal domestications of humped cattle, millets, and legumes, but these do not negate the significance of the external flows. Indeed, Hoque (2005) presents some thought-provoking information from Gangetic archaeological surveys: the middle valley has 15 recorded Neolithic sites, but 134 Chalcolithic, whereas the lower valley, to the contrary, has 99 Neolithic settlements and only 77 Chalcolithic. I detect in this a gradual movement downstream, between 3500 and 2000 BC, of westerly Chalcolithic populations of Indus/Early Harappan cultural inspiration, mingling with easterly Neolithic populations, perhaps of separate lower Gangetic or Southeast Asian origin and probably rice-growing. The latter should have been at their highest densities in the strongly monsoonal regions of Orissa, Jharkand, Bihar, and Bengal, rather than in the drier upper Ganges basin, and it is precisely in these areas that Munda-speaking populations still exist in greatest numbers today (Anderson 2008).

All of this implies that the Harappan urban civilization housed large populations of IE (Indo-Aryan) speakers, and probably Dravidians too, since north-western South Asia is a likely homeland region for the latter in terms of Dravidian subgrouping and place name substrata (although Southworth 2006 prefers a homeland more to the east). This is not the place to ask whether the Harappan symbol system (mnemonic notation or script?) was thereby the oldest attested Indo-European potential writing system, pre-dating Hittite and Linear B Greek by

almost 1,000 years. But, interestingly, Kenoyer (2006) traces the origins of some of the Harappan symbols into Hakra Phase sites in Pakistan, early in the fourth millennium BC.

Where did the Hakra Phase people come from? The 5,000 years of cultural continuity from this period onwards into early historical and modern times in the upper and middle Ganges Basin surely renders these people speakers of IE (Indo-Aryan?) languages, at least in Haryana and by association in the Indus region as well, given the theoretical position taken in this presentation that major language spreads were associated with movements of their speakers. Related IE (Indo-Iranian?)-speaking populations must have existed in Iran at the same time, even though the oldest *philological* evidence for their presence in Iran and Syria (Mitanni) does not pre-date 2000 BC, and is mostly very much later. One observation that can be drawn from this is that historical and philological documentation need have nothing to do with ethnolinguistic origin – a lesson that I believe the Hittites also teach us. Like the Iranians, the Hittites have long been regarded by many archaeologists and linguists as having been recent migrants into Anatolia when they first appeared in history, early in the second millennium BC, on the grounds that the relevant texts also refer to people in the vicinity speaking unrelated languages such as Hattic and Hurrian. But these texts do not prove at all that the Hittites were migrants, just as the Rigveda does not refer to an actual migration of people into South Asia from the west. These historical texts are irrelevant (or only tangentially relevant) from an origins perspective. If the Hittites were not natives of Anatolia, then neither comparative IE linguistics nor archaeology throw any light at all on their origins.

Any discussion of Indo-Iranian/Indo-Aryan origins within the IE family inevitably brings up the whole issue of the overall origin of ancient Indo-European-speaking populations. I have given my basic opinion in *First Farmers*. In terms of modern comparative linguistic studies that include extinct subgroups such as Anatolian and Tocharian, the linguistic origin region can be placed in Anatolia, as suggested by Colin Renfrew in 1987 and supported more recently by the computational and genealogical IE subgroupings of Warnow (1997), Ringe *et al.* (2002), and Gray and Atkinson (2003). I remain unconvinced that any subgrouping argument within IE supports a Pontic steppes origin north of the Black Sea, and regard the arguments for this from linguistic palaeontology – especially from horse, cart, and wheel vocabularies (Anthony 2007, Parpola 2008) – as tangential to the real question of origins owing to the potential for early borrowing rather than absolute inherited cognacy in early phases of language family differentiation. Most of this vocabulary is anyway absent in Hittite, although I have no disagreement with Parpola's view that wheeled vehicles and their associated vocabulary items were innovated amongst IE-speaking communities.

For both Tocharian and the Indo-Iranian languages there are many who also argue for a central Asian steppes homeland, subsequent to that for the IEs as a whole, based on borrowings into early Uralic languages and isoglosses with Baltic and Slavic languages (e.g., Parpola 1994, Witzel 2003, Anthony 2007, Kuzmina

2007). But both Parpola (1994, 2008) and Lane (1970) note that the oldest identified innovations shared by Indo-Iranian and Tocharian are actually with Greek and Armenian, both located close to but south of the Black Sea and close to the Anatolian core region. Genealogical subgrouping evidence for a steppes source region appears to be completely lacking, and borrowings into early Uralic, even if from Proto-Indo-Iranian (as suggested by Witzel 2003), could reflect early Indo-Iranian excursions from the south, like those that led to the much later Scythian (presumed IE) presence north of the Black Sea recorded by Classical authors. Herodotus (Book 4, chapter 11), interestingly, derived the Scythians from south of the Araxes River that separates Armenia, Iran, and Turkey. Furthermore, the borrowings into Uralic can only be identified as *exclusively* Proto-Indo-Iranian if they can be shown to be innovations *absolutely* unique to that subgroup.

The idea of a steppes origin for the Indo-Iranian and Tocharian languages forces some linguists and archaeologists to argue that cultures such as the Yamnaya, Afanasievo, Sintashta, and Andronovo belonged to ancestral speakers within these two linguistic subgroups (Witzel 2003, Anthony 2007, Kuzmina 2007, 2008). Yet all of these cultures, especially the late and more easterly ones with their punctate stamped and incised pottery styles and pastoral/horse-using economies (Kohl 2007), seem to me quite unrelated to the painted pottery and undoubtedly agricultural complexes reported from Neolithic and Bronze Age southern Turkmenistan, Iran, and northern South Asia, a point made also by Hiebert (1994) and Lamberg-Karlovsky (2002:74). There seems to be little archaeological evidence for such southwards movement prior to the Andronovo culture of the second millennium BC, in my view far too recent in time and anyway very different, as Hiebert and Lamberg-Karlovsky both note, from the contemporary Bactria–Margiana and Iranian archaeological complexes to its south.

Why not allow the Turkic speakers some role in the Neolithic prehistory of the steppe regions of central Asia? They are usually excluded completely from discussions of Neolithic ethnogenesis in this region on the assumption that their only expansions were those recorded in early Medieval history and that they were somehow hiding far away in northern Mongolia prior to this time. I am not convinced by this at all, neither, obviously, is Lamberg-Karlovsky (2002), and the Turkic center of gravity in linguistic terms lies firmly in a vast zone of central Asia between the Caspian Sea and the Altai Mountains (Golden 1998). The idea that the Turkic speakers occupied the whole of this territory *only after* replacing Iranian speakers since 2,000 years ago needs to be examined carefully on the basis of comparative linguistic reconstruction, rather than on the common observation that the recorded Turkic languages are not deeply differentiated, a situation that could simply reflect historically recent expansions, not ultimate origins.

If we allow an IE homeland in Anatolia at 7000 BC, rather than in the Pontic steppes at 3500 BC, then the whole chronology for IE history in Iran and South Asia is lengthened, and we no longer need to rely on the Rigvedic date of the second millennium BC for Indo-Iranian arrival. The two Tocharian languages are only distantly related to Indo-Iranian, and given their location in Xinjiang it must

be assumed that at one time there were ancestral languages further west, now presumably swamped by Indo-Iranian and Turkic languages. The Nuristani languages of the eastern Himalayas are considered by some linguists to be coordinate with the Indo-Iranian subgroup (see discussion in Cardona and Jain 2003), and the *centum* status of Bargani (like Tocharian) within Nuristani is of interest (Witzel 2003), but none of this can explain Tocharian without further support. My assumption, however, is that IE languages of some type, but perhaps not strictly Indo-Iranian ones, should go back quite deeply into Chalcolithic or even Neolithic times in Iran and Pakistan.

I am here giving strong support to Renfrew's 1987 "Hypothesis A", and infer that languages ancestral to both Tocharian and Indo-Iranian are likely to have spread eastwards, presumably in chronological succession rather than together, from Neolithic Anatolia, via Armenia, across northern Iran and into southern Turkmenistan and Afghanistan, before entering Pakistan by at least 4000 BC. I see no reason why the initial Neolithic occupations in this region, such as those at Jeitun and Mehrgarh I, should not have been IE-speaking, although I was reluctant to acknowledge this in *First Farmers*, just as Renfrew tended towards caution in 1987. Serious research is needed on the relationships between the Early Harappan material culture of South Asia and its contemporaries and predecessors further west. The Namazga I painted Chalcolithic pottery at Altyn Depe in Turkmenistan (Masson 1988) is of particular interest for possible Early Harappan parallels, since it dates to about 4000 BC and may well have belonged to a tradition that extended back to Jeitun at 6000 BC (Kohl 2007:218). Hiebert (1994) favors continuity from the Bactria–Margiana Archaeological Complex back into at least Namazga III in Turkmenistan, at about 3500 BC.

The view presented here would have the historical Indo-Iranians attested in classical sources and place names on the Pontic steppes (Scythians, Sarmatians) as migrants who spread north, perhaps long after the initial Indo-Iranian dispersal began. The primary movements eastwards of Indo-Iranians and Tocharians occurred to the south of the Black and Caspian Seas, and a case can now be made from both archaeology and linguistics for a derivation from the general region of Anatolia. Indeed, new observations of a catastrophic drowning at about 6300 BC of the extensive lowlands that once fringed a freshwater and much smaller Black Sea (Turney and Brown 2007) could be of great potential interest. Even though an archaeological record for the freshwater Black Sea is still lacking, due to a drowning of all potential sites at a depth of 155 m, it is possible that extensive human populations derived from forebears in the Anatolian Neolithic could have lived around its shores, to be expelled as salt water drowned the agricultural lowlands. Some of these populations, before the catastrophe but subsequent to the initial break-up of Proto-Indo-European at c. 7000 BC, and separate from the ancestral Tocharian and Italo-Celtic communities, could have included still-undifferentiated ancestral Balto-Slavs, Indo-Iranians, and Armenians within one large innovation-linked (rather than innovation-defined) Indo-European linguistic subgroup. If the flooding encouraged them to move in search of new land to north

and southeast, much within Indo-European deep history could be explained, even if at this stage this can be little more than speculation. What we need now is a far deeper consideration of the archaeological and historical linguistic landscapes of eastern Anatolia, Armenia, northern Iran, and Afghanistan.

If we turn to the human genetics to see whether this interpretation can be supported, we find, as with the Austronesians and Uto-Aztecs, that it is more a case of reinforcing one hypothesis against the other, rather than ruling one or the other out completely. In the case of South Asia, recent mtDNA and Y research has supported related ancestries for the populations of northwestern South Asia and populations located in the Middle East and Europe (Cordaux *et al.* 2004a,b, Quintana-Murci *et al.* 2004). This picture is given quite strong support by a new genome-wide analysis of 650,000 SNPs (Li *et al.* 2008), wherein selected populations in central and southern Asia, the Middle East, and Europe cluster quite tightly when compared with all other tested populations. Within South Asia, however, this analysis only tested populations from northwestern regions, mainly Pakistan, including the Dravidian-speaking Brahui.

Some geneticists dispute any western or central Asian connections for Indian populations. Sengupta *et al.* (2006) have noted that there is relatively little central Asian Y-chromosome input into South Asia, and use this observation to minimize the impact of Indo-European migration. But, of course, from my perspective this is perfectly acceptable, since steppe-region central Asians nowadays are not Indo-European-speaking anyway and probably never have been. Another anti-migration suggestion by Sahoo *et al.* (2006), that South Asian Y-chromosome lineages, apart from the Middle Eastern J2, are all pre-Neolithic, is presumably based on an assumption of an Indo-European presence since only 1500 BC, on molecular clock assumptions, and again on analysis of mostly non-IE-speaking peoples in the rest of Asia. In the absence of any ancient DNA research, the current picture for northern South Asia from human genetics is ambiguous, but it appears not to rule out a substantial degree of shared ancestry with populations located in western Asia.

Perhaps it should be pointed out, finally, that this perspective on the spread of Indo-Iranian languages east of the Fertile Crescent need not be in total conflict with all previous opinions. Witzel (2003), for instance, presents a careful layering of borrowings from non-IE languages into Indo-Iranian through time. I do not doubt that these borrowings occurred, or that some Indo-Iranians (yet not the original ones) maintained a former presence in or close to the central Asian steppes, or even that comparisons of the Old Iranian and Old Indo-Aryan vocabularies allow reconstructions of words for horses, chariots, and spoked wheels. All that I am arguing is that the composers of the Avesta and the Rigveda were not the first IE speakers east of the Fertile Crescent, and that those who were (ancestral Tocharians perhaps?) entered the region via Iran rather than from somewhere between the Volga and Yenisei Rivers. The Avesta and the Rigveda were composed at a time of great cultural and demographic expansion of certain sectors of the Asian Indo-European community, and it is not at all surprising

that the languages associated with these two epics should have undergone very considerable linguistic aggrandizement at the expense of predecessors, both IE and non-IE alike. Finally, it is not necessary to argue that IE speakers were the only inhabitants of Neolithic and Chalcolithic Iran, apart perhaps from some early Elamite populations in the southwest, although I am constrained to suggest that if the Harappan were IE-speaking, even if only in part, then the BMAC is likely to have been similarly endowed, given its close overlap in time, space and ideology with the Harappan (Parpola 2008 also suggests this, but from a different perspective).

3 Conclusions: how and why did agriculture spread?

The archaeology and comparative linguistics behind all three case studies, as interpreted here, allow for agriculture to have spread essentially through population growth and dispersal of farming populations, incorporating indigenous hunter–gatherer groups in the cultural and linguistic senses. The genetic evidence is rather more ambiguous but does not rule such an explanation, particularly when expressed through the classic mechanism of demic diffusion, which does not demand population replacement. One can add additional causal factors, such as boats and good winds to carry along the Austronesians, but such additions hardly rate as foundation causes.

It is also apparent that these dispersal episodes occurred after agriculture had become well attested, both from comparative linguistic reconstructions of inherited farming vocabularies and from the archaeological recovery of domesticated plants and animals. In my view, a demographically fueled movement of existing agriculturalists was the driving force in each case, carrying both the domesticated species and the languages. But hunter–gatherer adoptions of agriculture, and maybe also farmer languages, occurred gradually in marginal terrains where farming spread was difficult, particularly if the demographic profiles of the farmers and the hunters were reversed, as may have occurred round the eastern fringes of the US Southwest and in far western and northern Europe. Hunters and gatherers would also have found it easier to adopt elements of food production if their lifestyles were fairly sedentary, as might have been the case in rich coastal habitats.

The questions of most significance for the Harlan II conference revolve around the movements of the domesticated crops and animals themselves. In most cases, I detect that they moved with their “owners” through population spread, but of course there were also many occasions of movement as gifts or commodities, particularly in later periods of history. What is striking to me is the length of time that food production required to spread through situations of environmental change. The spread from Mesoamerica to the Southwest was fairly rapid since climatic parameters were similar all the way, but that from the Indus into the Ganges Basin involved movement from a winter rainfall into a summer rainfall

monsoonal climate, hence a time lag of perhaps 3,000 to 4,000 years. A similar time lag hedged the spread of farming from the temperate Yangzi Basin into tropical Southeast Asia, and from Mediterranean Anatolia to the temperate edges of northwestern Europe. This suggests to me that independent forager adoptions of agriculture, solely via interaction across group boundaries, and in situations where no farmers were already present, played little role in prehistory. But let us not forget conversely that erstwhile hunter-gatherers, independently in several regions of the world, developed the food-producing lifestyle in the first place!

Note

1 Dates are in calendar years, derived where available from calibrated radiocarbon determinations.

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8 California Indian Proto-Agriculture: Its Characterization and Legacy

M. Kat Anderson and Eric Wohlgemuth

Despite the fact that California Indians lived, gathered, hunted, and managed lowland oak ecosystems for millennia, the land was productive enough in the 1860s to support a new and very intensive land use: modern agriculture. Drawing from an existing legacy of the Indian era – its fertile soils, biodiversity, conserved water, and abundant timber resources – modern agriculture flourished. This chapter characterizes the indigenous food cultivation and management systems that were in place in California’s lowland oak ecosystems at European contact.

Harlan (1992:242) reminds us that to develop a sustainable agriculture, “We need to approach the daunting tasks ahead with more humility and take a broader view of the ecosystems we must manage”. Following Harlan, we suggest that indigenous manipulation of plants for food *not* be viewed in isolation, but rather in a broader context of prehistoric subsistence systems and how these systems fit within and impact dynamic and diverse ecosystems. For example, wildlands contain plant resources for fuel, weapons, clothing, basketry, cordage, tools, dyes, and medicines. Yet vegetation manipulation to augment wild plant populations for these needs is seldom considered in tandem with food getting. By focusing upon one cultural use category, we argue that the multi-dimensionality of human traditional ecological knowledge remains obscured. Native people are viewed as preoccupied with “getting food”, rather than understanding the structure and function of ecosystems and how they can be modified to provide for all of their needs.

We propose that the investigation and analysis of California Indian–oak ecosystem interactions be conducted within an ecosystems management framework. We argue that California Indians were far more than passive hunter–gatherers. They were in fact proto-agriculturalists, practicing both vegetation management and cultivation, so successful in their management that for the most part they did not degrade their resource base. Proto-agriculture can be defined as the practices promoting the growth and/or reproduction of native plants, some of which are incipient domesticates, by methods of cultivation. As defined here, proto-agriculture is not necessarily a transitional state to full domestication or field agriculture; rather, it can be a long-term stable adaptation

(see Smith 2001). Field agriculture can be defined as the growing and harvesting of domesticated crops in fields by methods of cultivation that usually, but not always, involve systematic tillage of the soil.

1 California Indians and the hunting and gathering spectrum

The majority of California Indian tribes at European contact were not growing domesticated crops, but rather living by hunting, fishing, and gathering many kinds of plants. Except for tribes in southeastern California who grew domesticated crops in the fertile flood plains of the Colorado River Valley, most California tribes have been tagged “hunter–gatherers” (Figure 8.1). In more recent years, the dichotomization of hunting and gathering and agriculture has been replaced with the concept of a continuum of human–plant interactions – from gathering, to encouragement, cultivation, and domestication (Ford 1985, Harris 1989). Hunter–gatherers are now viewed as encompassing a wide range of lifeways, and in some cases, they can claim an intermediate spot on the continuum because they enhanced and intensified food resources by practicing various forms of resource and land management, coupled with more sedentary lifestyles and higher population densities (Kelly 1995, Smith 2005). Jack Harlan (1992:23) was one of the first scientists to assert that most hunter–gatherers are similar to agriculturalists by pointing out that the main contrast between foraging and farming is that “no plant used by hunter–gatherers is completely domesticated, otherwise hunter–gatherers do about everything farmers do”. In California, native people manipulated plant and animal resources to meet their needs in ways that came to resemble the cultivation of domesticated plants in agricultural societies (Anderson 2005a).

The rich body of traditional ecological knowledge and management practices that underlie domestication is a likely explanation for why there are many and diffuse origins of domestication throughout the world (Harlan 1995:15). The gathering and hunting way of life in the world was not only the most persistent but also the most successful adaptation that humans have ever achieved (Harlan 1992:4). We would also argue that it is precisely this knowledge and these practices that made hunter–gatherers so successful in adapting to and shaping their environment, not their lack of intervention in these “pristine” ecosystems as the earlier hunter–gatherer stereotype would suppose.

2 Original California ecosystems that became modern agricultural landscapes

Harlan (1992:242) challenges us to take a broader view of the ecosystems we must manage, looking to natural ecosystems for guidance. If we do that in the context of modern agriculture, we must ask: What were the original ecosystems

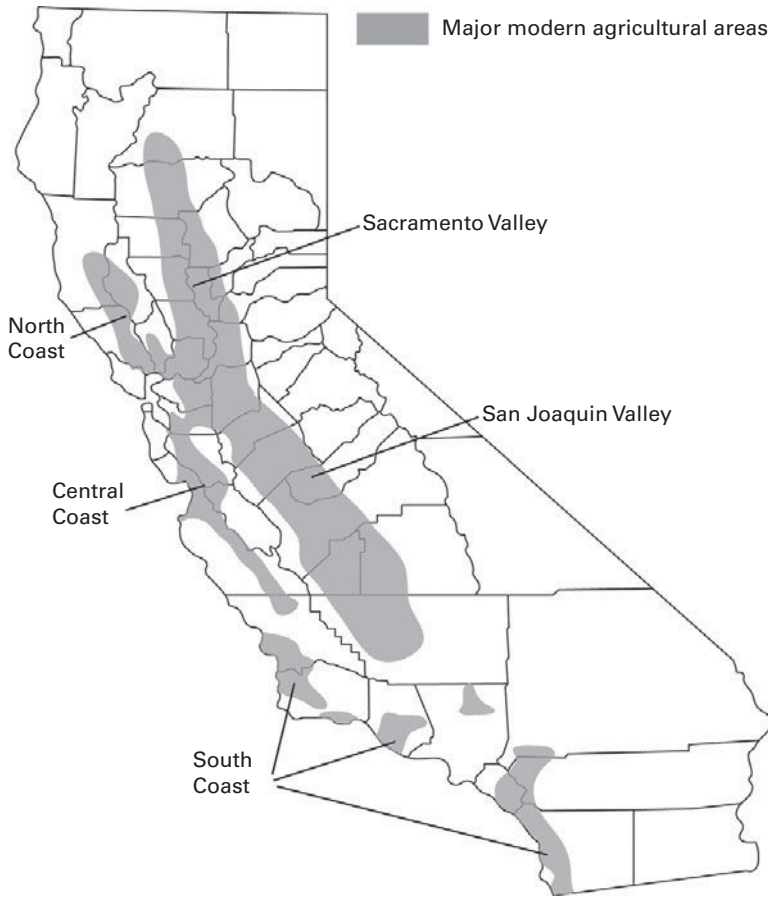


Figure 8.2. Major modern agricultural areas in the California Floristic Province (Scheuring 1983).

that were the birthplace of modern agriculture? The five major modern agricultural regions of the California Floristic Province, the Sacramento Valley, the San Joaquin Valley, the North Coast, the Central Coast, and the South Coast (Figure 8.2), are embedded in what were once oak landscapes with widely spaced large-diameter trees interspersed with an understory of grasses and forbs (Figure 8.3). These landscapes were vividly described by T.C. Jones in 1882: "...the great valley of Sacramento and San Joaquin, extending a distance of no less than 350 miles from north to south, and containing about 14,000 square miles – a vast level plain, mostly dotted over with native oaks, which, with their low and expanding branches and evergreen foliage, make this region one of enchanting beauty, and it is of extraordinary fertility for the production of this great world-recognized standard cereal [wheat]" (Jones 1882). The growing of wheat between Willows and Fresno starting in the 1860s provided "a transition economy" to a more lasting agriculture in California (Starr 1985).



Figure 8.3. Harvesting hay in the Sacramento Valley, 1915. Courtesy of UC Davis Special Collections.

It is no coincidence that the places that became the best modern agricultural lands were highly desirable as indigenous homelands (Figure 8.4). These areas are relatively flat, in the lowlands with good water resources, high-quality alluvial soils, and abundant plant and animal resources (Starr 1985). There was human occupation by various groups in these areas continuously for 13,500 years (Jones and Klar 2007).

The best modern agricultural regions correlate with very high Indian population densities at European contact (Figure 8.5). For example, in Courtland, south of Sacramento, there were an estimated 16.5 people per square mile at contact. In the Santa Barbara region the Chumash achieved a density of 20 people per square mile (Milliken 2006, John Johnson, pers. comm. 2008). These figures contrast with the next highest population density of 5 people per square mile among the Kongkandji in Australia and the Puyallup in Washington. Some California tribes had achieved the greatest population densities of any hunter-gatherer group on Earth at the time of European contact (Kelly 1995:222–6).

3 Gathering the biodiversity in oak landscapes

Oaks were the most important of all native nut trees to California Indian traditional economies, and acorns were the principal staple of the tribes in the areas that were to become the best modern agricultural lands (Figure 8.6). The major oaks used in these areas include valley oak (*Quercus lobata*), coast live oak (*Q. agrifolia*), interior live oak (*Q. wislizenii*), California black oak (*Q. kelloggii*), blue oak (*Q. douglasii*), Engelmann oak (*Q. engelmannii*), Oregon oak (*Q. garryana*), canyon oak (*Q. chrysolepis*), and the tan oak (*Lithocarpus densiflorus*) (considered a true oak by California Indians) (Pavlik *et al.* 1991). The use of acorns is very

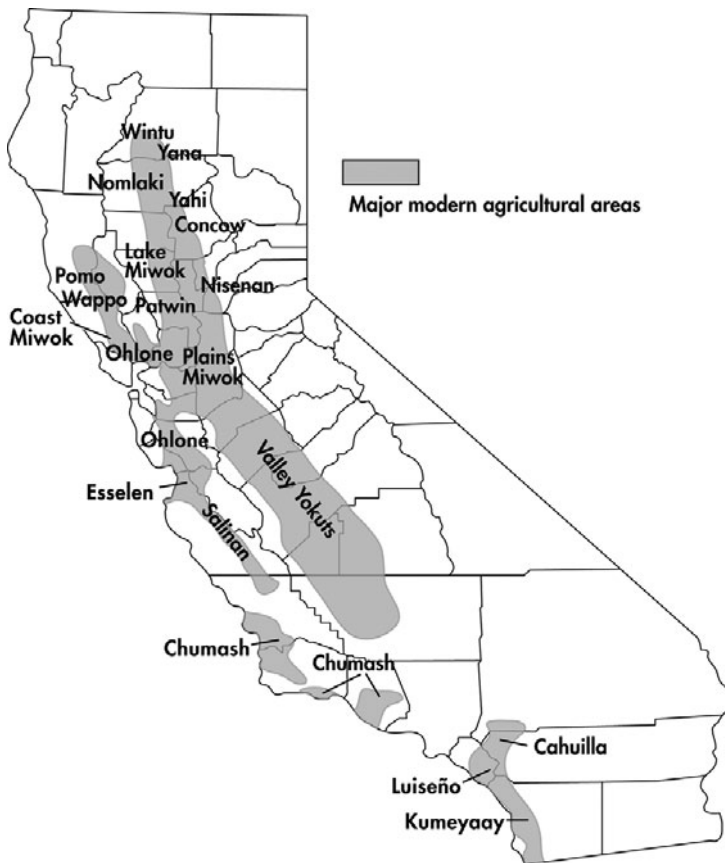


Figure 8.4. Major modern agricultural areas overlaid with tribal territories at European contact.

ancient, dating to 7400 to 9900 BP east of Mt. Diablo and 7800 to 10,200 in the central Sierra foothills. Three to five thousand years ago there was a gradual intensification of the use of acorns to the point where it became the principal dietary staple in interior central California (Figure 8.7). Acorn nutshell is the most abundant charred plant food residue in archaeological sites in all regions of central California (Wohlgemuth 2004).

Today many tribes still highly value acorns and acorn collection gives them continuity with their past and a long-term association with places, strengthening tribal ethnicity (Figure 8.8). A widespread rule that is still in place today is: “Never take all acorns from any one tree. Always leave some for the other animals”.

Although oak trees were of immense cultural value to tribes, the productivity of these landscapes lay not only in the trees, but also in the understory herbaceous flora composed of forbs and grasses. Plants were harvested for medicines, cordage, household items, basketry, and many other uses.

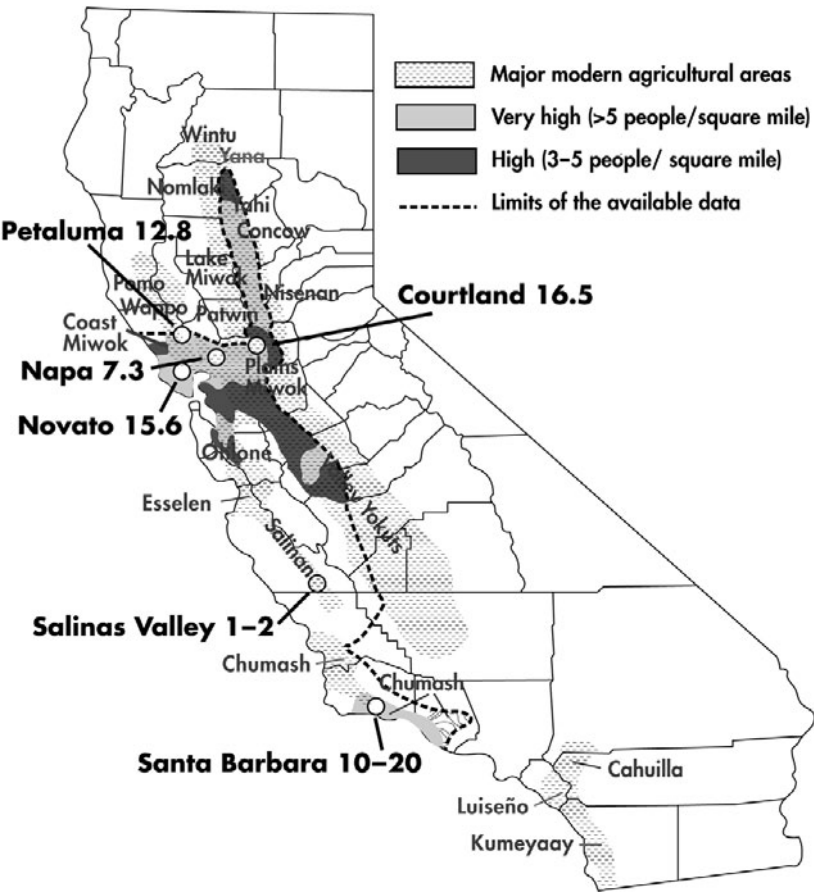


Figure 8.5. California Indian population densities at European contact.



Figure 8.6. Historic photograph of Letah Garcia (Wukchumni Yokuts) with shelled acorns. Frank Latta Collection, courtesy of Yosemite National Park Archives, Library, and Museum.

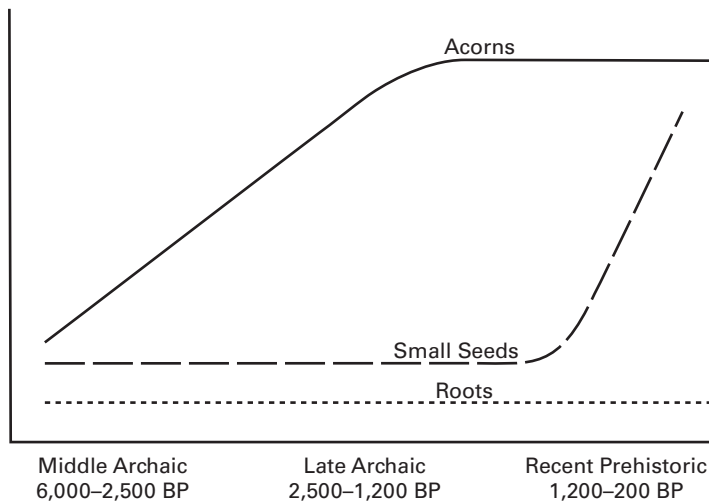


Figure 8.7. Trends in prehistoric plant use in interior central California (Wohlgemuth 2004).

California Indians harvested a broad spectrum of plants for foods. The California Indian diet was rich in plant diversity. Each tribe utilized several hundred species found in their territories. Cumulatively, the number of species utilized statewide adds up to just over one thousand species; about one-sixth of the native flora was exploited for their bulbs, leaves, fruits, or seeds.

From oral interviews and the ethnohistoric and archaeobotanical record, we know that openings between the oak trees provided patch sites for gathering many kinds of forbs and grasses (Du Bois 1935, Latta 1977, Wohlgemuth 2004, MK Anderson, unpublished field notes, 2006–2007). Forbs such as brodiaeas (*Brodiaea* spp., *Dichelostemma* spp., and *Triteleia* spp.), mariposa lilies (*Calochortus* spp.), and sanicles (*Sanicula tuberosa*) were dug with digging sticks for their edible bulbs, corms, tubers, and roots. Forbs with edible leaves and stems (greens) such as California thistle (*Cirsium occidentale*), miner’s lettuce (*Claytonia perfoliata*), and fiddleneck (*Amsinckia* spp.) were pinched, torn, or cut. Marie Cohoe, Mono (pers. comm., 2006), describes how California thistle was harvested (Figure 8.9): “The thistle is gathered in spring when young in the early stages and is broken off or cut with a knife. It is eaten raw. Take off the leaves and peel the stem. Then eat the stem raw. My mom taught me how to eat the thistle.”

About a thousand years ago people clearly intensified their use of small seeds in interior central California. Red maids (*Calandrinia ciliata*), farewell-to-spring (*Clarkia* spp.), and tarweeds (*Madia* spp.) among others were gathered for their small edible seeds (Table 8.1). This intensification of wild plant resources, both acorns and small seeds of grasses and forbs, is likely linked with the high densities of Indian populations (Wohlgemuth 2004).

Ruby Pomona, North Fork Mono (pers. comm. 2007), describes the harvesting of red maids seeds in the Central Valley (Figure 8.10): “Kaseen has black seeds that were gathered by grandma Lizzie. They were parched or roasted and pounded



Figure 8.8. Grace Tex, North Fork Mono, cooking acorn mush. Photograph by Kat Anderson, 2006. (Ms. Tex turned 100 years old in April 2009.)



Figure 8.9. Marie Coho, Mono, remembering how to harvest the greens of California thistle (*Cirsium occidentale* var. *californicum*). Photograph by Kat Anderson, 2006.



Figure 8.10. Ruby Pomona, North Fork Mono, holding two native forbs with edible seeds: bluehead gila (*Gilia capitata*) on the left and red maids (*Calandrinia ciliata*) on the right. Photograph by Kat Anderson, 2006.



Figure 8.11. Melba Beecher, Mono, holding *Sagayu* (*Lyophyllum decastes*), an edible mushroom that is gathered in the fall after the rains. It grows under blue oaks (*Quercus douglasii*), interior live oaks (*Q. wislizenii*), and California black oaks (*Q. kelloggii*). Photograph by Kat Anderson, 2006.



Figure 8.12. Lois Conner (North Fork Mono/Chuckchansi) harvesting soaproot (*Chlorogalum pomeridianum*) by breaking off the root crown and leaving it behind in North Fork where it had been burned the year before. She says: "Where it has been burned I find plants that are doubles, triples, and bigger clusters and the bulbs are huge." Photograph by Kat Anderson, 2008.



Figure 8.13. Soaproot crown left in the ground. Photograph by Kat Anderson, 2008.

Table 8.1. Common small-seeded plants in archaeological sites of interior central California

Common name	Taxon	Ubiquity ^a
Goosefoot	<i>Chenopodium</i> spp.	62.8
Canary grass	<i>Phalaris</i> spp.	54.8
Farewell-to-spring	<i>Clarkia</i> spp.	50.9
Fescue	<i>Vulpia</i> spp.	49.1
Hairgrass	<i>Deschampsia</i> spp.	41.3
Red maids	<i>Calandrinia</i> spp.	40.6
Fiddleneck	<i>Amsinckia</i> spp.	38.2
Brome grass	<i>Bromus</i> spp.	30.2
Bedstraw	<i>Galium</i> spp.	29.2
Wild barley	<i>Hordeum</i> spp.	28.9
Tarweed	<i>Madia</i> spp.	27.9
Buttercup	<i>Ranunculus</i> spp.	20.4
Miner's lettuce	<i>Claytonia</i> spp.	17.8
Tule	<i>Scirpus</i> spp.	17.1
Saltbush	<i>Atriplex</i> spp.	12.7
Phacelia	<i>Phacelia</i> spp.	10.3
Peppergrass	<i>Lepidium</i> spp.	10.9
Clover	<i>Trifolium</i> spp.	8.3

Note:

^a Ubiquity is percent of samples in which taxon is present of total interior central California samples ($n = 396$).

in a mortar hole. The flour was moistened with manzanita cider and shaped into a ball about the size of a spaghetti meatball. It was eaten any time of day.”

Grasses such as fescues (*Vulpia/Festuca* spp.), canary grass (*Phalaris* spp.), native barley (*Hordeum* spp.), blue wild rye (*Elymus glaucus*), and witchgrass (*Panicum capillare*) were harvested for their grains (Wohlgemuth 2004, Anderson 2005b). The seeds and grains of many of these forbs and grasses were harvested with a seed beater, a shallow basket with a handle. California Indians purposefully scattered seeds around the plants, in addition to collecting them, to perpetuate the seed stock, acting as seed dispersers (Voegelin 1942, Anderson 2005a).

3.1 Legumes

A wide variety of useful native legumes grew in areas that were to become the best farmlands in California. These legumes spread out over wildlands as herbaceous vines, annual and perennial herbs, erect bushes, and small trees. Early Spanish, Mexican, and American accounts mention the abundance and diversity of legumes in grasslands and oak savannas. Wild pea vines (*Lathyrus* spp.), for example, covered wide areas of level ground with such a tangled growth that it was difficult to walk through it and horses tripped over the vines (Chesnut 1974:357). Early writings describe a “sea of blue” referring to the ubiquitous lupines (*Lupinus* spp.),

that according to Eugene Hilgard (1900:225) covered the ground “for miles.” Wild clovers (*Trifolium* spp.) flourished (Bryant 1985:314), along with vetches (*Vicia* spp.), milk vetches (*Astragalus* spp.), bird’s foot trefoil (*Lotus* spp.), and leatherroot (*Hoita* spp.). These were all very prevalent when the first farms and ranches were established.

The genera listed above were useful to Native Americans in many ways, and provided ecological services to their surroundings by fixing nitrogen. Tribes made string and rope from their roots and used their foliage to insulate their houses, thatch their roofs, and line their acorn granaries. Their chemical properties aided in the treatment of many kinds of ailments. Indian tribes ate their seeds and leaves (Sparkman 1908:231, Nomland 1935:155, Schenck and Gifford 1952:385, Bean and Saubel 1972:121, Bocek 1984:250, Collier and Thalman 1991:121, Shippek 1991:31). Some of the legumes were significant enough to be labeled a common food and even stored over the winter (Barrett and Gifford 1933, Latta 1977:622). V.K. Chesnut noted in the late 1800s that the vine American vetch (*Vicia americana*) “was common in grassy fields and brush throughout the region” and that it was gathered by the various tribes living in Mendocino County (probably including the Yuki, Wailaki, Concow, and Little Lake Pomo), who baked or boiled the vegetable stems when young and ate them as greens. Its stout roots also performed as cordage for tying things (Chesnut 1974:362). Botanist P.B. Kennedy in 1917 said that “. . . in early days before the great flocks of sheep traversed the State and the farmer commenced cultural operations, the valleys and hills were densely covered with one or other of the Spanish Clovers” (Kennedy 1917:35). These are the *Lotuses* of which there are thirty kinds. The young shoots and leaves of different *Lotus* species were eaten (Sparkman 1908:231, Barrett and Gifford 1933:144).

3.2 Mushrooms

Certain mushrooms that grow around oaks were quite useful to tribes in the form of foods and medicines. Some of the edible mushrooms harvested by California Indians include: *Tricholoma magnivelare*, *Amanita calyptata*, *Helvella lacunosa*, *Lyophyllum decastes*, *Morchella* spp., *Peziza sylvestris*, and *Ramaria* spp. (Heffner 1978–1984, MK Anderson, unpublished field notes, 2006–2007) (Figure 8.11). These all grow in tandem with oaks or tan oaks. Fungi were and continue to be an important part of the diet and there are certain rules adhered to when picking: (1) When harvesting leave the stipe behind; (2) Cover the area back up; (3) Leave the threads underground (the mycelia) undisturbed; and (4) Spare some mushrooms (MK Anderson, unpublished field notes, 2006–2007).

4 California Indians as proto-agriculturalists

Until recently, vegetation types in California were viewed as “natural” and their productivity maintained through natural disturbance in the complete absence of

human influence (Vale 2002). It is now recognized that many ecosystems often considered “natural” actually evolved through significant human influence and the ability of Native Americans to meet their needs was sustained through direct human intervention, involving a variety of vegetation management and cultivation techniques (Bean and Lawton 1993, Lewis 1993).

4.1 Vegetation management

Vegetation management can be defined as caring for native plants through such activities as knocking, pruning, weeding, protecting, watering, and/or burning, resulting in changes in plant abundance, diversity, growth, longevity, yield, and/or quality. A common practice up and down California was to collect acorns before they fell, knocking them out of the oak trees with long poles or climbing the trees and whipping the acorns down. There are dozens of references to this practice (Anderson 2009). Today native people gather acorns from the ground, but many remember the former practice of knocking. Native people stress that knocking is good for the trees and may in fact, be a form of management. Melba Beecher, Mono, says (pers. comm. 2006): “Knocking wakes the tree up. It alerts the tree to bear more.”

Another method by which acorns were harvested was by climbing the trees and cutting the limbs. Mono elder Lydia Beecher remembered the former pruning of oaks: “My grandpa Jack Littlefield would climb black oak trees and cut the branches off – just the tips so that many more acorns would grow the next year.” Knocking and pruning may have been beneficial to oaks in a number of ways: (1) Removal of dead and dying branches that could harbor disease; (2) Removal of oak galls and mistletoe; (3) Encouraging emergence of many new branches – increasing canopy surface area; (4) Increase of fruit production; and (5) Forestalling the impact of storms, which could otherwise break branches and disfigure the tree.

Of all the vegetation management techniques, burning was the most pervasive and effective technique for manipulating oaks and other vegetation. Harlan (1992:23) understood this fact and said that “fire was used to modify vegetation just about anywhere that vegetation could be burned, and the practice may well have gone back to Acheulean times. New shoots [following a burn], unencumbered by old growth attract grazing animals; the ash provides some fertility for re-growth; heat renders phosphorus more available; woody vegetation is retarded and herbaceous plants increased; wild seed harvests are enhanced; roots and tubers escape injury in the dry season and thrive as competition is reduced.”

Many tribes also set low intensity fires in oak landscapes to achieve a variety of goals: facilitating acorn collection; enhancing deergrass (*Muhlenbergia rigens*) for basketry material; stimulating the production of sprouts for the making of cultural items; reducing brush and decreasing the likelihood of major conflagrations that would destroy the oaks; suppressing diseases and acorn pests; encouraging the growth of edible mushrooms; increasing edible grasses and forbs between the oaks and in the surrounding forb-grasslands; driving game and grasshoppers; and

increasing forage for wildlife (Stewart 1935, Peri and Patterson 1979, Anderson 2005a). Tribes that burned include the Luiseño, Kumeyaay, Cahuilla, Chumash, Wintu, Wappo, Concow, Nisenan, Yana, Pomo, Valley Yokuts, Plains and Sierra Miwok, Salinan, Mono, and many others (Anderson 2005a, MK Anderson, unpublished field notes, 2006–2007).

Melba Beecher, Mono, and many other native elders and non-Indians whose families have lived in an area for a long time confirm burning around the oaks: “My grandfather Jack Littlefield burned the land. If there was a drought it would cause green sprouts to grow for the deer. It was better for all of the basketry materials and for the mushrooms growing under the pines. They burned in November under the incense cedars, black oaks, and pines. They would just let the fire go. The rain would just put it out. This produced new oak sprouts for stirring sticks for stirring acorn and for digging sticks that were harvested in late spring. The ashes made the acorn trees grow better. The ashes also killed the bugs that fed on the leaves, bark and acorns. It probably scorched the oaks but didn’t kill them. They burned every year. They’d take different sections. They would wait a few years to set a fire in the same area again” (pers. comm., 2006).

Eldon Pura (pers. comm., 2006), whose family came to the Greenfield area in Salinas Valley in 1910, recalls: “When the Salinan left an area they would burn it. They burned it to get the ground clear. When they came back the following year there would be grass there. They burned in the fall when the grass is dry. They burned every year. They would burn the same area if they came back to it. They burned in the open areas between the oaks.”

Burning was used as a biological control method for reducing insect infestations of acorns. The two insect genera that cause the most extensive destruction to acorns in most oak species in California are filbert worms, *Cydia latiferreana* (formerly *Melissopus latiferreanus*) and filbert weevils, *Curculio occidentalis*, *C. parvus*, and *C. aurvestis* (Gibson 1969:259). These insects can multiply and over time, few acorns would escape damage to become oaks. While the number of acorns produced and the insects feeding on them can vary from year to year for different kinds of oaks, scientists agree that they can pose significant impacts on the oak ecosystem (Swiecki *et al.* 1990). Native Americans harvested acorns with a keen eye to blemishes of any kind and those that exhibited insect damage were immediately discarded (Anderson 1993).

Gilbert Hanley (pers. comm., 2002), a long-time resident of Arroyo Seco, grew up with Salinan and Esselen descendants and says: “You look at the acorns now and I’d say that 40 to 50 percent of them have got insects in them. Well in the burning it eliminated those insects. The insects normally come up out of the ground and get into the oaks and become worms... That was one of their principal reasons for burning around them, to knock those insects off so the nuts were good nuts... he [Manuel Sullivan, Salinan] said every couple of years they’d just torch an area.”

Through burning, Indians managed the land on a larger scale, affecting the number, size, and species composition of oak groves. Indians set fires to enhance

plants with edible leaves and stems, many kinds of geophytes with edible underground swollen stems, forbs and grasses with edible seeds, and shrubs with fleshy fruits (Anderson 2005a). There is good evidence, for instance, that tribes burned areas to enhance the abundance of legumes and keep areas open. Tribes that burned to encourage legumes include the Wappo, Pomo, Mono, Wukchumni, Salinan, and Maidu (Duncan 1964:9, Beard 1979:52, Peri *et al.* 1982:119, Anderson 2005a, MK Anderson, unpublished field notes, 2006–2007).

4.2 Cultivation

Cultivation is defined as caring for plants through such activities as collecting and sowing seeds or grains and tilling (digging and replanting propagules) in a cyclical manner. It differs fundamentally from vegetation management in that it controls reproduction through selecting for which individuals are going to survive and reproduce and planting them in the ground under more favorable conditions.

4.2.1 Tillage

Indigenous people in California cultivated subterranean organs of wild plants for foods with a digging stick. This activity may be the oldest form of tillage, one that became the precursory management regime and provided the ecological foundation for the development of root crop agriculture in many areas (Anderson 2005c). When California Indians harvested geophytes through digging, they did more than just retrieve the largest bulbs, corms, and tubers for eating. They replanted the smaller bulblets and cormlets so that they could grow into new plants; they broke off the root crowns and left them behind; they aerated the soil to facilitate the growth of the new plants; and they scattered the seeds contained within the dried fruits to enhance sexual as well as asexual reproduction. In these ways, they practiced a kind of cultivation that allowed an annual harvest while facilitating the continued growth of a “crop” in subsequent years. Lois Conner (North Fork Mono/Chuckchansi) harvests soaproot (*Chlorogalum pomeridianum*) bulbs, an ancient food, and remembers what her Aunt Rosalie taught her: “dig soaproot after the plants go to seed and leave the roots behind. If you break them off, they will grow back again” (see Figures 8.12 and 8.13).

Through human selection, protection, and replanting of offsets, certain geophyte species may have undergone genetic changes. The excavation of plants with vegetative reproductive parts and the replanting or breaking off of such parts would likely select for specific genotypes that benefit under human disturbance regimes (Anderson 2005c).

4.2.2 Sowing seed

California provides many examples of tribes managing landscapes to foster the growth and abundance of herbaceous plants for edible seeds. The Modoc, East

Shasta, Pit River (Achomawi), Wappo, Chumash, Northern Maidu, and Nisenan tribes sowed the seeds of many kinds of wild herbaceous plants (Driver and Massey 1957, Beard 1979, Miller 1988). We can reasonably assume that the combination of burning and sowing of seed crops was understood and employed by most tribes because we have extensive documentation of burning areas, sowing, and tending of native tobaccos (Anderson 2005a).

4.3 Imitating natural disturbance

Over fifteen years ago Jack Harlan (1992:242) foresaw that closely imitating natural ecosystems was the only hope “for achieving stability and sustainability in our managed ecosystems.” Harlan (1992) suggested that we learn much about simulating nature from those individuals who had developed the arts of survival – traditional farmers. If we explore the origins of both vegetation management and cultivation – these activities may, in fact, be some of *Homo sapiens*’ first attempts to mimic nature. The vegetation management techniques of burning, pruning, and coppicing may be ingenious imitations of lightning, herbivory, and flooding. The cultivation technique of replanting propagules from edible geophytes, likely is a close simulation of small and large mammal predation and dispersal. Thus, humans were imitating natural disturbance with which native plants and ecosystems have become adapted, and in some cases co-evolved.

Disturbance is a recurrent feature of virtually every vegetation type in California (Christensen 1988). We hypothesize that indigenous disturbance was so finely tuned and similar to certain types and scales of natural disturbance that it conserved the renewal capacity of individual plants, populations, and whole ecosystems. For example, with regard to vegetation management, setting fires, pruning, and coppicing likely simulated flooding, herbivory, and lightning fires (Figure 8.14). Many of the wild plants best suited for indigenous use for basketry, traps, weapons, fencing, walkways, weirs, and structures in California and elsewhere are dependent on disturbance to rejuvenate their populations. But the grade and quantity of young branches produced after natural disturbance are far superior to undisturbed growth. Undoubtedly, California Indians linked natural disturbances with the creation of these higher quality and quantities of plant material for use, and special conditions for certain plants to thrive.

In Europe, woodlands and savannas were coppiced or pruned for hundreds or thousands of years, creating a plant architecture that fostered small-size poles and brushwood for fuel, fodder, charcoal, thatch, fencing materials, roads, basketry, and hand tools (Buckley 1992, Joffre *et al.* 1999, Terradas 1999). Similarly, California Indians lit surface fires, pruned, or coppiced shrubs and trees to activate these same growth forms. Within as little as six months after an Indian-set fire had blackened an area, a shrub or tree was transformed. Crooked, gnarly, insect-ridden branches become new, insect-free, and pliable shoots up to 2 m tall. These sprouts were harvested for at least ten categories of cultural items

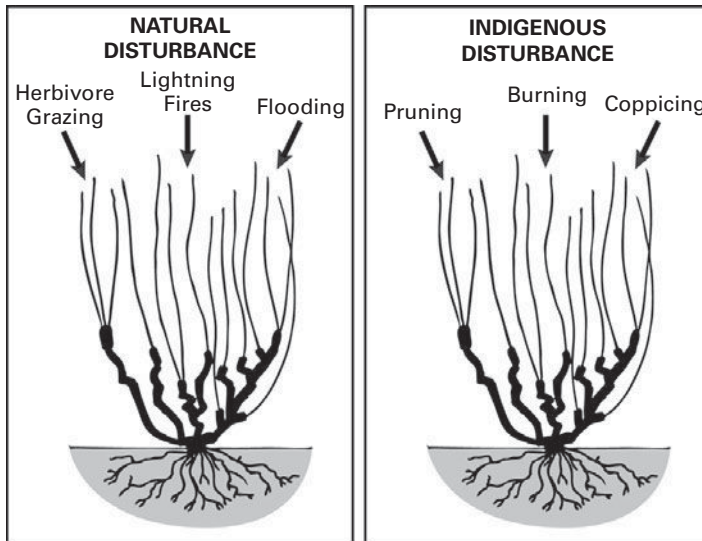


Figure 8.14. California Indian burning, coppicing, and pruning promote long, straight sprouts with no lateral branching imitating the natural disturbances – lightning, flooding, and herbivory, which also activate this same plant architecture.

for many different kinds of objects including headdresses, rod armor, traps, whipping sticks, cordage, spears, baskets, arrows, looped stirring sticks, granaries, and musical instruments. In both the British Isles and California, the same genera were managed, including hazelnut (*Corylus* spp.), oaks (*Quercus* spp.), and willows (*Salix* spp.) (Buckley 1992, Terradas 1999).

Humans have long known that the grade of the plant material affected the function of a manufactured item for human use. The morphology and age of a branch for an arrow, or the uniformity, age, and straightness of branches for constructing a watertight basket will greatly affect the aerodynamic properties of the arrow, or whether the basket will indeed hold water. For example, an arrow cut from buttonwillow (*Cephalanthus occidentalis*), by a Yokuts Indian in California would not be straight, long, dry evenly, or be aerodynamic – flying straight to the target – without management by burning or pruning.

Evolving in environments in which herbivory, fire, and drought were common, geophytes all developed clonal structures – offsets or propagules in the form of bulb scales, bulblets, or cormlets – which if severed or otherwise separated from the parent structure could grow into new plants genetically identical to the parent (Sauer 1952:25). With this kind of adaptation, disturbances (especially herbivory) that might threaten the existence of the parent plant was also likely to separate and disperse the propagules, ensuring the continuation, if not the multiplication, of the genome. Feasting upon these highly nutritious bulbs, and severing the propagules to grow into new plants, gophers, ground squirrels, bears, deer, and elk would simultaneously act as predators and dispersers. Through cultivation – digging plants in areas and replanting bulblets and cormlets – Indians simulated mammal

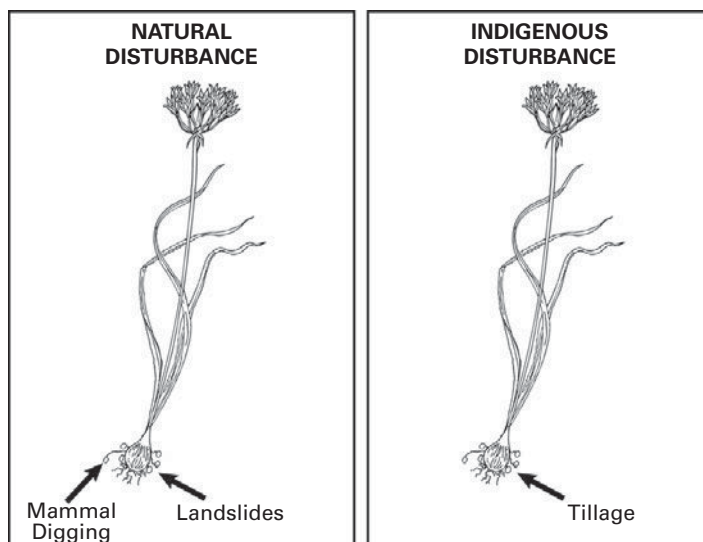


Figure 8.15. California Indian digging of geophytes with digging sticks in areas and replanting bulblets and cormlets imitate mammal disturbance and landslides, which also disperse propagules.

disturbance (Figure 8.15). Thus, native people who exploited geophytes as food were simply stepping in to the herbivore role, taking advantage of the pre-existing adaptations that made most geophytes excellent subjects for food intensification strategies (Thoms 1989, Anderson 1997, Anderson and Rowney 1999, Ames 2005).

The native peoples of California could intensify underground storage organs because they could apply human observation and analysis to the process and then pass on what they learned to future generations through human culture. With digging sticks, native people could deliberately soften and aerate the soil, keep it from compaction, and re-level the surface, whereas bear and elk employing snouts, paws, and hooves would leave holes and re-compact the soil with their weight. Aerated and loosened with digging sticks, the soil probably had a higher moisture-holding capacity and became a better environment for seed germination and propagule growth. Native people could also pay attention to plant density, preferentially harvesting the densest patches to keep the plants from getting too clumped, and thus maximizing production. Perhaps most importantly, native people could make conscious decisions about what to harvest and what to leave behind, based on accumulated knowledge about the plants' reproduction, and they could deliberately separate propagules from the parent structures instead of leaving the separation to chance.

5 A new conceptual model for California Indian–nature interactions

Richard Ford (1985) and David Harris (1989) have proposed that plant–human interactions with regard to prehistoric food production be conceptualized as a

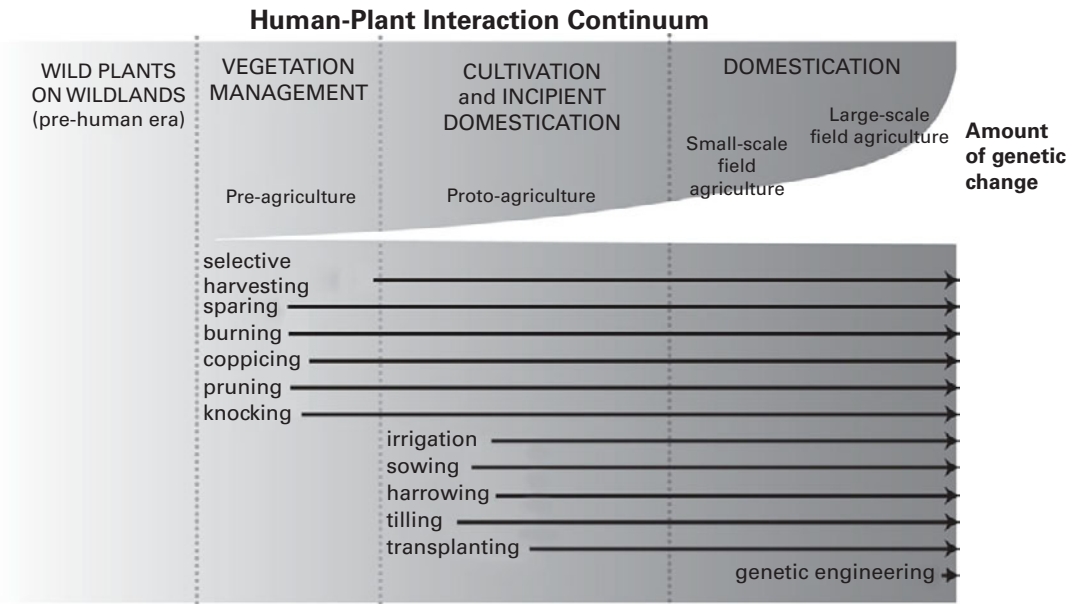


Figure 8.16. Human–plant interaction continuum. The distinction between “wild” and “domesticated” in plant exploitation is not a sudden or marked change; it is a gradual transition. Native American tribes in California did not domesticate crops, yet they still managed and cultivated wildland environments with an array of techniques causing changes at different scales of biological organization. They operated in the middle of the continuum. (Adapted from Harris 1989 and Ford 1985.)

continuum whereby the dichotomy of hunter–gatherer/agriculturalist is blurred and the focus is upon the diversity and interrelations of activities through which people have, in the past, exploited both “wild” and “domesticated” plants and animals. We agree that human–food plant interactions should be appropriately viewed as a continuum from gathering to tending, to cultivation, to domestication. Indigenous peoples in California and the Pacific Northwest operated in the middle of this continuum (Figure 8.16) (Smith 2005).

The continuum of human-induced vegetation change processes from vegetation management to domestication can also be conceptualized as three major stages on a gradient of ecological change induced by human modification – the pre-agricultural stage, the proto-agricultural stage, and the field agricultural stage. For example, in areas where plant domestication and the practice of agriculture never occurred, long-term cultivation practices with wild plants could still very likely lead to genetic changes that make plants better suited to the conditions of human-disturbed environments – such as burned-over areas – and less adapted to the conditions of natural environments. The pathway that leads to seed domestication, for example, is probably a similar one in different areas. This pathway starts with selection pressures on plants in areas that are harvested repeatedly. Further along the pathway to vegetation change is the actual burning of areas,

preparation of soil, sowing of seed and/or replanting of propagules, and harrowing. These activities can, over time, favor specific features of the seed or plant, and produce faster or more robust growth, which favors survival and flourishing with reliable production to the point where full domestication is not necessary. Yet, the evolutionary modifications are significant enough to lead to incipient or intermediate states of domestication, resulting in proto-agriculture. It can be postulated that systems of edible bulb and seed production of hunter–gatherer groups in many parts of the world evolved to a point on the continuum of human–plant interaction that stopped short of the endpoint of full domestication (Figure 8.17) (Anderson 2005c, Smith 2005). Thus, domestication is but one kind of biologically defined symbiotic relationship, and the manipulation of wild plants for edible bulbs or seeds are examples of many other types (Rindos 1984).

Possible evidence of the genetic changes in native plants due to indigenous management and cultivation is the fact that many plants that were used for native foods thrived in farmers’ fields as weeds in 1890 (see Table 8.2) (Dyer 1891, Hilgard 1891). We postulate that non-Indian horse-drawn tillage and planting in fields created similar habitats to Indian digging, sowing, harrowing, and burning. Edgar Anderson (1954) and Nikolai Vavilov (1926) both concluded that most domesticates are open-habitat plants. Anderson (1954) noted that such plants readily mutate when grown in disturbed soils. Hilgard (1891:240), wrote of the tenacity of red maids in modern agricultural fields, a forb whose seeds were important as a native food in large areas of the state (Figure 8.18): “...the *Calandrinia menziesii* (now *Calandrinia ciliata*), does not give up so readily and may be seen covering the ground in orchards and vineyards in the coast region, forming a beautiful carpet of purple that attracts attention from afar. Its vegetative duration is too short and its root system too light to render it troublesome; but the multitude of its shining black seeds render it difficult of extirpation.”

What is missing from the continuum concept is how getting food fits into a total scheme of human–environmental relations within each specific ecosystem. We propose to conceptualize and analyze native peoples’ past interactions with nature within an ecosystems management framework (McNeely and Scherr 2003). We are suggesting that in reconstructing historical human–land relationships, one has to look at human activities using concepts and methods developed in ecology. Ecosystem management is the idea of management of whole systems for a variety of purposes rather than simply for production of a single resource type like “food” or “timber”. It differs from older approaches in that the researcher investigates how human activities affect ecosystem processes and structural elements, as well as outputs. In the past researchers concentrated on studying outputs (what did native peoples get from the natural environment?) What we are most interested in is the question: Were human land use and management activities designed to sustain ecological systems; and if so, how? Our overarching hypothesis for low-land oak ecosystems is that Indians maintained ecosystem health.

Within this framework, different cultural groups in different time periods would not be simply distinguished by an either/or proposition (either they practiced

PROTO-AGRICULTURAL STAGE (preceded by Pre-agricultural Stage)

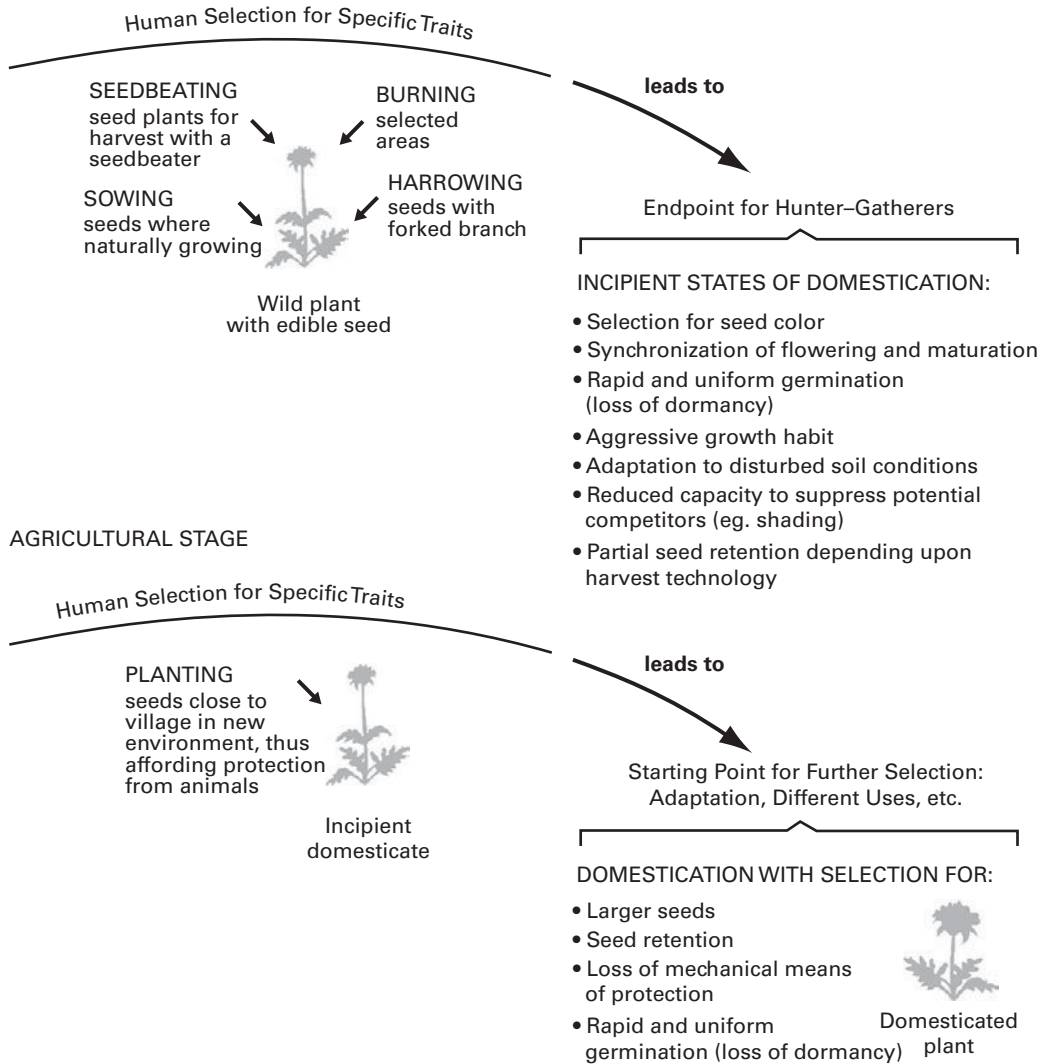


Figure 8.17. The continuum of human-induced vegetation change from gathering to domestication can be conceptualized as three major stages on a gradient of ecological change induced by human modification. These stages are not clear-cut, but grade into each other. The diagram does not imply that given enough time, hunter-gatherers would advance from one level of interaction with plants to the next. (The pre-agricultural stage is not represented here.) Figure reproduced, with permission from CRC Press, from Anderson (2005c); permission conveyed through Copyright Clearance Center, Inc.

agriculture or they didn't), but rather the detailed particulars of their interactions, from the organism to the landscape scale, would be unraveled. The questions that would frame this approach, asked by ethnobiologists, archaeologists, and ecologists, would center around sustainability issues. In other words, how do past

Table 8.2. Common weeds in farmers' fields in 1890

Asterisks indicate plants common in archaeological sites.

Plant species	Useful part	Cultural use
Blow wifes (<i>Achyrrachaena mollis</i>)*	Seeds	Food
Coast tarweed (<i>Madia sativa</i>)*	Seeds	Food
Common madia (<i>M. elegans</i>)*	Seeds	Food
Clover (<i>Trifolium gracilentum</i>)*	Leaves	Food
Fiddleneck (<i>Amsinckia intermedia</i>)*	Seeds and leaves	Food
Hayfield tarweed (<i>Hemizonia congesta</i> var. <i>luzulifolia</i>)*	Seeds	Food
<i>Layia</i> spp.	Seeds	Food
Lupine (<i>Lupinus bicolor</i>)	Seeds and leaves	Food
Mariposa lily (<i>Calochortus invenustus</i>)	Bulbs	Food
Miner's lettuce (<i>Claytonia perfoliata</i>)*	Leaves	Food
Red maids (<i>Calandrinia ciliata</i>)*	Seeds	Food
Saltgrass (<i>Distichlis spicata</i>)	Salt crystals on plant	Food
Sanicle (<i>Sanicula bipinnatifida</i>)	Tubers	Food
Yerba mansa (<i>Anemopsis californica</i>)	Rhizomes	Medicine

human actions and their effects fit into a current view of natural disturbance? A current view of nutrient cycling? A current view of primary productivity? A current view of maintenance of biological diversity? Research questions and hypotheses would be developed and a range of methodologies from diverse disciplines would be utilized to track the archaeological record of past human environmental manipulations and harvesting strategies and to test their resulting ecological impacts with field experiments at different levels of biological organization.

6 Tracking proto-agricultural practices in the past

While the focus of this chapter is on the rich ethnohistoric and ethnographic record of Indian plant management and cultivation, it is important to keep in mind that such practices represent a highly evolved system. Early Holocene groups had low population densities and moved frequently over large territories. It was not until 3,000 to 5,000 years ago that contact-era hallmarks of intensive acorn use and sedentism arose, and this was restricted to the richest regions (see regional prehistory summaries in Jones and Klar 2007). We might predict that more intensive proto-agricultural practices would be associated with higher population densities and the intensification of more costly foods of the past 3,000 to 4,000 years, and would increase further in importance toward the recent end. Moreover, these practices should be most conspicuous in regions with the most elaborate archaeological records and highest population densities, such as the Santa Barbara mainland coast, the San Francisco Bay Area, the southern North Coast Ranges, and well-watered areas of the Sacramento and San Joaquin valleys.

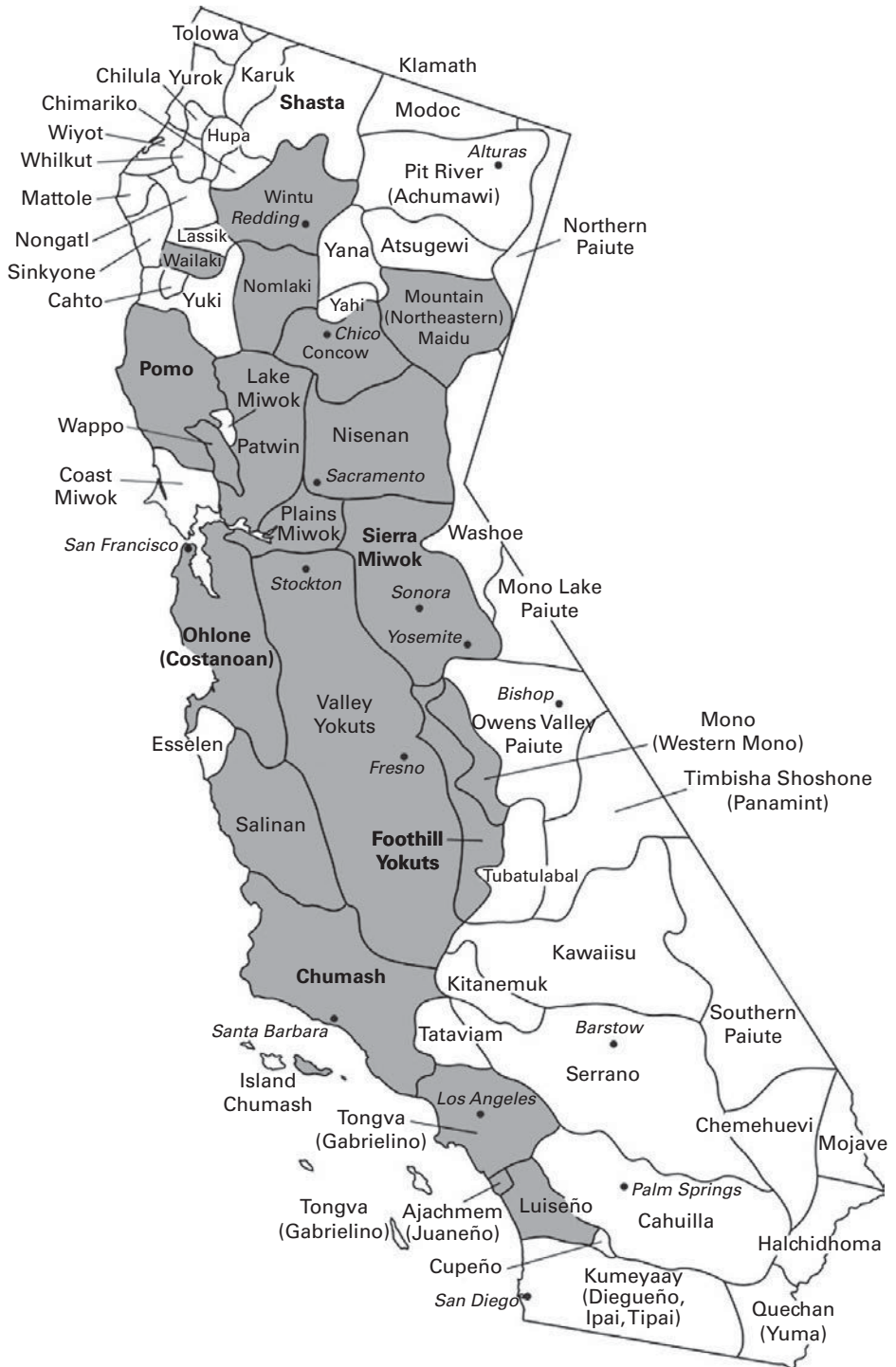


Figure 8.18. Widespread use of red maids (*Calandrinia ciliata*) for their edible seeds among tribes (in gray).

Table 8.3. Proportion of frequency of disturbance-follower small-seeded plants by time period from interior central California

Period	Middle Archaic	Late Archaic	Recent Prehistoric 1	Recent Prehistoric 2
Age (years ago)	7,000 to 2,500	2,500 to 1,000	1,000 to 500	500 to 200
Proportion	67.2%	75.2%	66.3%	68.0%

Comparison of archaeological plant and animal remains from long cultural sequences within similar habitats would provide the framework to establish whether more intensive plant gathering, management, and cultivation arose later in time. Below we list research issues and archaeological data that may address the evolution of proto-agricultural practices in California.

Does the archaeobotanical record display signatures of managed burning? Hammett (1991) attempted to find such a signature in archaeobotanical data from southern California, but found no direct evidence of managed burning at historic Chumash village sites in Santa Barbara and Los Angeles counties. Abundant small seeds (particularly of legumes), along with bulbs and corms, from a small Recent Prehistoric site in coastal dunes in northern Santa Barbara County was cited as possible evidence of managed burning. However, since natural processes, notably severe weather and high winds, and intensive grazing by native artiodactyls, can also create extensive disturbance in dunes, this finding is not necessarily conclusive. The simple presence of disturbance-follower plants in archaeological sites (see Table 8.1) does not necessarily imply use of managed burning to promote them; disturbance-follower small seeds have been found in the central California record since the Early Holocene (*c.* 9,000 BP, Wohlgemuth 2004). Moreover, Hammett’s sample suffers from a critical lack of time-series data from similar habitats.

The archaeobotanical record of interior central California, a densely populated region, includes robust data for the past 5,500 years, with more tenuous information for prior periods (Wohlgemuth 2004). We predict greater use of disturbance-following small seeds through time that would be promoted by managed burning. Specifically, if managed burning is tracked by increased frequency of all small seeds, then it would have been more important after AD 1000, when small seeds increase dramatically in archaeological sites (Wohlgemuth 2004).

Here we test this hypothesis using an index focusing on disturbance-following small-seeded plants whose production could be increased through managed burning. This index is the proportion represented by disturbance-following grasses and forbs of the total number of small seeds. Table 8.3 shows these values by time period. Counter to the hypothesis, these data do not show any trend that suggests increased use of disturbance-following small seeds late in time. The proportion of disturbance-following small seeds is more or less stable, and actually declines slightly with the increase in small seeds after AD 1000.

The absence of correlative increase in disturbance-following small seeds during Recent Prehistoric increased use of all small seeds may have its roots in the

classification of plants as disturbance-followers or not; some may be mischaracterized, such as canary grass, here not viewed as a disturbance-follower (although if canary grass is included as a disturbance-follower, the proportions show even more stability through time, ranging from 80.2% to 83.5%). There may also be the issue of scale, where local variability in herbaceous small-seeded vegetation within interior central California (e.g., Kruckeberg 2006) may obscure trends that might be visible in comparing time-series data from a single locality. But if these data are accurate, native Californians have always focused small-seed gathering on disturbance-followers. Rather than a feature of a densely populated region, a regular burning regime may have been part of the California landscape since at least the Middle Archaic. Small-group mobile foragers typical of the Middle Archaic could have significantly transformed the landscape through burning, similar to low-density groups in Australia (Lewis 1989, Bowman 1998). One fire set by a single forager could burn large areas and significantly improve habitat for disturbance-followers. Alternatively, managed burning may have had little effect on disturbance-follower distributions, although this seems implausible given the burned grasslands extending for miles reported near the coast by eighteenth-century Spanish explorers (Minnich 2008).

The apparent stability in use of disturbance-followers accompanying the dramatic increase in use of all varieties of small seeds after 1,000 years ago suggests that the effects of managed burning did not increase after that time, and therefore this practice does not account for increased small-seed use in interior central California. Some other factor(s) must have led to increased importance of small seeds in late prehistoric times. Contributing factors may include a new gathering technology, such as the advent of seed-beating, or green-stage bulk-gathering and processing. Wohlgemuth (2004) rejects seed-beating due to the historic occurrence of woven seed beaters in areas lacking evidence of intensive small seed use, but suggests the dramatic Recent Prehistoric increase in inedible capsule of farewell-to-spring (*Clarkia* spp.) may in part reflect increased green-stage gathering. Another intriguing alternative is sowing edible plant seeds after fires (see *Cultivation* section above for ethnohistoric accounts), which is particularly interesting in light of recent studies of seed size of two important California grasses.

Saving and sowing wild seed on small plots could lead to reproductive isolation and perhaps enlarged seeds, which appears to be the initial stage of the evolution of domesticate characters for grasses (Fuller 2007). There is tantalizing ethnohistoric and archaeobotanical evidence that this may have occurred in California. Bean and Lawton (1993) and Shipek (1993) hypothesize use of large-seeded grasses from observations by Spanish explorers in coastal Orange and San Diego counties. Hammett (1991) and Miksicek (1999) made initial studies of large-seeded grasses in Morro Bay and Davis, respectively, but were hampered by lack of local comparative diachronic data. While native barley (*Hordeum* spp.) is abundant in archaeological sites on the Orange County coast, no trends were noted toward larger-seeded caryopses through time (Klug and Popper 1998). A pilot study spanning most of a 4,000-year sequence from the lower Sacramento Valley

suggested that seeds of canary grass and native barley may have become larger in the terminal prehistoric record (400 to 120 years ago; Wohlgemuth 2004). Reddy's (2009) initial study of native barley from Ballona Lagoon in Los Angeles County, showing larger caryopses from historic Mission period Native American deposits than from Intermediate Period (3,000 to 1,000 years ago), confirms the real possibility of native horticultural practices late in time. Such practices need to be verified in the late central California record, but suggest that seed sowing may explain at least part of the substantial increase in small seeds after AD 1000.

While further seed-size studies of potential domesticates are critical, canary grass and native barley were initially cited as domesticates in the prehistoric American Midwest not on the basis of increased seed size, but from pure or near-pure finds in caches or features similar to other known domesticates (Asch and Asch 1985). Concentrations of both of these grasses have been found in sites along Ballona Lagoon (Reddy 2009), but not in central California, where they are found mixed with several abundant small-seeded taxa (Wohlgemuth 2004). However, goosefoot (*Chenopodium* spp.) is singularly abundant in interior central California Late Archaic archaeological sites, comprising more than one-quarter (27.8%) of all small seeds. While goosefoot seed has always been common in interior central California sites, its dominance during the Late Archaic suggests it might have been cultivated. Domesticate characters of goosefoot such as thin seed coats (Smith 1995) found elsewhere in the world should be assayed for the entire central California sequence, focusing on the Middle to Late Archaic transition.

While the charred seed data apparently suggest a long history of managed burning, there may be other data sets that could confirm its time depth. Shifts in faunal assemblages might show a reduction in perennial vegetation cover as managed burning became more prevalent. Studies in the American Southwest have shown a shift from earlier use of cover-seeking brush rabbits (*Sylvilagus audubonii*) to open-country jackrabbits (*Lepus californicus*) with the transition to increased agricultural field clearing (Szuter and Bayham 1989). Similar shifts may have transpired in California localities where both animals occur. Additionally, high-resolution noncultural sediment records may have implications for prehistoric fire frequency. To date, charcoal in such records has been largely mute on the frequency of fires as a potential index of managed burning in the lowlands; charcoal from varved off-shore deposits in the Santa Barbara Channel show no increase in frequency over the past 560 years (Mensing *et al.* 1999). In the Sierra Nevada charcoal frequency is variable, declining after 5,000 years ago in some locales (Brunelle and Anderson 2003), after 2,000 years ago in others (Smith and Anderson 1992), but increasing after 1,200 years ago in still others (Anderson and Smith 1997).

The history of other proto-agricultural practices might also be investigated. Can we detect more intensive tillage cultivation of geophytes later in time? Are more recent charred corms of the *Brodiaea* group larger, as tillage may have become more regularized and systematically encouraged the growth of larger corms? Can we see changes in archaeological faunal assemblages that signal

biological control of competitors for valued geophytes, such as increased frequency of bones of rodents, bear, or artiodactyls?

Proto-agricultural practices other than burning may be less visible or invisible altogether in the archaeological record, such as pruning oak branches and knocking acorns from oak trees. Some, such as coppicing shrubs and tending sedge root patches to improve basketry materials, are unlikely to leave definitive macrobotanical signatures, depending on our capacity to identify basketry material waste archaeologically.

7 Testing proto-agricultural practices today

Because many of the most productive modern farms are located within former oak ecosystems, and these landscapes were not biologically impoverished at European contact despite millennia of Native American use, it behoves us to study the former Indian–nature interactions in these oak ecosystems to learn how their practices may have led to sustainability. Since indigenous management and gathering practices were refined over periods of perhaps thousands of years, they can be a source of ideas, principles, and strategies complementing a scientific approach to agricultural and wildland conservation management. Below are some of the questions we can begin to ask and research directions designed to quantify and qualify indigenous systems, emphasizing some of those areas such as, biodiversity, cover cropping, soil conditions, carbon sequestration, and biological control of animal pests of greatest interest to farmers and ranchers today.

7.1 How might a multiplicity of useful plant species affect resilience in lowland oak ecosystems?

California Indians harvested many plant and animal species from lowland oak ecosystems. Production of one single plant species was not maximized at the expense of all others. Research could involve utilization of regional floras, archaeobotanical research, and herbarium specimens, in conjunction with detailed ethnobotanies of different tribes, to reconstruct plant species use, harvesting, and management lists assigned to lowland oak ecosystems, amassing an ethnobotanical database tailored to each region. Then ecological field experiments could be conducted that plant different sets of mixtures of useful species in lowland oak ecosystems under low- and high-rainfall years, investigating how this biodiversity affects ecosystem productivity and nutrient retention.

7.2 How does indigenous gathering of plant parts of native plants affect the future abundance of the plant part, and plant population?

Plant uses can be linked with cultural objectives for quality and quantity of plant parts (e.g., non-wormy acorns; first-year old shoots for basketry; large bulbs with

abundant old leaf sheaths around the bulbs used for brushes). These objectives translate into desired future conditions. Thus, it is possible to reconstruct, experiment with, and ultimately reintroduce approximate gathering, management, and cultivation regimes – season, frequency, extent, and intensity – which most successfully achieve these cultural objectives (Anderson and Rowney 1999).

7.3 How does indigenous gathering of plant parts of native plants affect carbon sequestration in lowland oak ecosystems?

Ecological field experiments could be set up to determine how Indian simulated gathering methods for select species affect carbon sequestration through measuring change in the plant's root : shoot ratios, nutrient cycling, decomposition rates, and productivity (photosynthetic rates).

7.4 How might the vegetation management practices of knocking, pruning, and burning affect acorn production and canopy development in oaks?

Studies could be designed in which oaks are knocked with knocking sticks, or pruned, simulating indigenous practices, paired with oaks that are left alone, measuring acorn production and numbers and diversity of terrestrial vertebrates, before and after these practices are applied.

7.5 How effective is Indian burning as a biological control strategy for insects that attack acorns?

Reconstruction of Indian burning regimes in combination with information on an insect's life history characteristics may help managers evaluate the effectiveness of simulated Indian burning for biological control.

7.6 How did indigenous harvesting and management of shrub and timber resources for fuelwood with fire, pruning, and coppicing affect their renewal capacity?

Long-term autecological studies could be set up to study the life history and physiological response of a shrub or tree species to burning, coppicing, and pruning.

7.7 How might the indigenous harvesting and management of legumes affect nutrient cycling within oak ecosystems?

We surmise that legumes played an important ecological role in oak ecosystems. They replenish soil nitrogen, an essential element to all plants in the system. We hypothesize that diverse native legume species were essential to the renewal of oak ecosystems. Ecological field experiments could be set up to determine the degree to which differences in indigenous harvesting and frequency of burning have any effect on nitrogen-fixation of legumes.

7.8 How do indigenous burning regimes affect mushrooms and mycorrhizas in lowland oak ecosystems?

Studies could be designed to measure changes in mushroom numbers, mushroom genetic diversity, and changes in mycorrhizal populations with simulated Indian burning regimes.

7.9 How does indigenous burning of legumes affect soil microbial communities?

Different kinds of ecological field experiments could be conducted such as the seeding of native legumes, known to be useful to California Indians, into grassland areas and then measuring their effects on soil microbial communities (Potthoff *et al.* 2009). Additionally, the effects of simulated Indian burning on legume population numbers and soil microbial communities could be studied.

8 Indigenous wisdom in modern agriculture

It would be naïve to think that there are simple solutions from California's indigenous past to the problems we are tackling in agriculture today. However, certainly more research funding and attention needs to go into the exploration and development of ethnobotanical uses of our native flora, especially potential food crops that could broaden the genetic and ecological base of our food supply (Prescott-Allen and Prescott-Allen 1986). Eating a broad number of plants native to California offers multiple options and insurance in the face of global climate change (Kingsnorth 2007). As native people have demonstrated, many of the edible plants are nutritious and do well in cultivation. Acorns, for example, are low on the glycemic index and if brought back into the native diet could help prevent diabetes, the fourth leading cause of death among Native Americans (Kar *et al.* 2001).

Early on, the University of California Agricultural College tested the food potential of some of our native plants, such as the potential of *Madia sativa* for its oil-yielding properties (Hilgard 1882). Many other kinds of products could come from the habitats supporting farming systems. The roots of the native dock, *Rumex hymenosepalus*, were grown in the 1890s in the University Experimental Garden at Berkeley and tested for tannins (Bonner 1891:123). Early national pharmacopeias, formularies, and dispensaries also incorporated California Indian medicinal plants such as gumweed (*Grindelia camporum*) (formerly *G. robusta*); the leaves were used by Indians and non-Indians alike for the healing of sores (Miller 1928). As early as 1889 the US Secretary of Agriculture suggested that experiments be set up for osier growing and coppicing of native willows for basketry enterprises on farms and ranches – modeled after California Indian use and horticultural practices.

In addition to products, the native flora could serve other kinds of functions – such as ecological services on the farm (Jackson *et al.* 2007). California's earliest university researchers were thinking along these lines. The native legumes may



Figure 8.19. Rancher John Wick of Nicasio, California, poses in a meadow barley (*Hordeum brachyantherum*) pasture with bales of hay made of this native grass. The hay makes livestock feed and is used for erosion control. Photograph by his wife Peggy Rathman, 2008.



Figure 8.20. Teacher and homemaker Elizabeth Barnett, of Inverness, with homemade muffins made with the native grain California brome (*Bromus carinatus*). Photograph by Kat Anderson, 2008.



Figure 8.21. Judith Lowry, proprietor of Larner Seeds in Bolinas, California, serving oatmeal with red maids seeds and wild huckleberries (*Vaccinium ovatum*). Photograph by Peter G. Smith, 2008.



Figure 8.22. Teacher and artist Rebecca R. Burgess, leading a dye workshop at Drake's Beach, Point Reyes National Seashore, using native plants as dye stuff for local fiber. Photograph by M. Kat Anderson 2011.

show promise as cover crops. The University of California Agriculture Experiment Station at Berkeley in the 1890s grew native lupines, *Lupinus affinis* and *Lupinus bicolor*, to measure their agricultural value for green manuring of crop lands. *Lupinus affinis* especially proved to be a valuable plant for green-manure in frostless regions, producing an abundance of tubercles both in new soil and in soil that had been manured. Its heavy yield per acre and great succulence led one researcher to encourage farmers to spread lupine-enriched soils over the surface of farmlands that lacked inoculation of soil and harrow or cultivate it with lupine seeds (Davy 1900:210, 219).

Today, some ranchers, small business owners, and homeowners are experimenting with the virtues of California's native plants in new and old ways, testing their food value, their forage potential for livestock and for erosion control, and their efficacy for dyeing textiles (Figures 8.19–8.22).

By studying the cultures that did not fully domesticate plants or adopt field agriculture, we believe that we can gain a greater understanding of the underpinnings or foundation upon which field agriculture rests. According to historian Martin Renner (pers. comm., 2008), “Highly productive native tree crops could improve local food ways, and agricultural sustainability while also mimicking natural ecosystems.” For example, oaks in California support 300 vertebrate species and 5,000 invertebrate species. Indigenous gathering and tending techniques with native plants might serve the dual goals of resource production and the conservation of biological diversity on the farm, contribute in major ways to carbon sequestration to combat global warming, and lead to the design of sustainable agroecosystems that resemble the managed “natural” ecosystems of the Indians.

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Section II

Domestication of Animals and Impacts on Humans

Thomas Famula

I cannot imagine a compilation of manuscripts, as are outlined in this monograph, that would not repeat in one form or another, the notion that plant and animal domestication is the most important development in human history. Were this not true, then why even develop the Harlan II symposium? And yet, for all its well-accepted importance, so many crucial questions about the nature, direction, speed, and origins of these domestication events remain unanswered. However, as this volume so amply illustrates, now is a marvelous time to be a scientist (or indeed a nonscientist) with even a tangential interest in this topic. The chapters of this section, on the domestication of animals, and the impact of these events on human populations, bear ample testimony to this interest.

Chapter 9 begins our journey with an outline of the possible pathways animals may have taken to domestication. Focusing on behavioral attributes of domesticates, in contrast with nondomesticates, this chapter helps us see the many pathways to the present: there is no “one-size-fits-all” approach to domestication of animals. Accordingly, today’s advanced genetic tools may help elucidate the biological phenomena exploited in these pathways. Examples are provided that chronicle commensal relationships between animals and humans, extension of the predator–prey path to domestication, and the utility of animals for some special value.

Chapter 10 continues this exploration. In this review, we see the application of a variety of genetic tools to help us investigate the exploitation of mutations, pre- and post-domestication. Discussing examples in the pig, chicken, and the horse, this work provides a clear and easily understood description of the evaluation of genomic data and the insight this information brings to questions about domestication.

Along this line of investigation, Bridgett vonHoldt *et al.* in Chapter 11 extend the concepts outlined in Chapter 10 with a case-study of the dog. Although the relationship of modern dogs to the gray wolf has been a point of discussion for many years, this work extends our understanding of this formative relationship.

As she and her colleagues describe, a dominant component of the dog genome derives from Middle Eastern wolves. These results are integrated with molecular data from dog breeds and canids across the globe, providing an informative analysis of the genetic isolation of dogs and wolves.

We finish this section with a report on human evolution, an evolution facilitated by the domestication of animals and cereals. Loren Cordain *et al.* outline the relationship of adult lactase persistence to the selection pressures of malaria in sub-Saharan Africans in [Chapter 12](#). This research proceeds to build a case for a similar advantage of lactase persistence in Northern Europeans over nutritional rickets, a disease likely to be aggravated by the high-cereal diets in these cultures coupled with the lower exposure to ultraviolet radiation in northern latitudes.

Taken together, these chapters outline a dominant theme in current research on the domestication of animals: evaluating the context of animals in early human societies and bringing the tools of modern genetics to bear on these enduring questions.

9 Pathways to Animal Domestication

Melinda A. Zeder

Jack Harlan was a polymath. His life-long study of crop evolution combined plant sciences, archaeology, systematics, genetics, and conservation, leaving a legacy of five decades of influential publications that explored all aspects of crop plants – their origins, their dispersal, and their continued and future role in supporting the Earth’s burgeoning populations. To Harlan, agriculture was not an invention or the product of a single big idea. Instead, he saw agricultural origins in terms of a long co-evolutionary process involving humans and plants that grew out of “many independent tentatives in many locations that fused over time to produce effective food production systems” (Harlan 1995). Harlan’s remarkable body of published work contains only one short encyclopedia entry on the subject of animal domestication (Harlan 1994). He was, in fact, somewhat dismissive of the contribution of animal domesticates to humankind’s food supply stating that “(a)nimals are not essential, plants supply over 90% of the food consumed by humans” (Harlan 1995). Jack Harlan would likely agree, however, that understanding livestock evolution requires the same breadth of focus that he brought to the study of crop evolution. Here I follow Harlan’s example in a consideration of domestic animals, bringing together information from animal sciences, genetics, and archaeology to explore the multiple pathways leading to animal domestication and the implications of these pathways for current and future relationships between humans and their animal partners.

1 Domestication as a process

All considerations of domestication, whether focusing on crops or livestock, acknowledge that it involves a two-way relationship between humans and target plant or animal populations. There is less unanimity in different conceptual approaches to domestication on whether emphasis should be placed on the human or the plant/animal side of the equation (see Zeder 2006a). Some cast humans as the dominant partner in a relationship in which humans consciously

and with deliberate intent assume “mastery” over all aspects of the production, movement, feeding, and protection of the domesticate (Hale 1969, Ducos 1978, Bökönyi 1989, Clutton-Brock 1994). Others see domestication as a form of biological mutualism in which both partners (humans and domesticate) reap benefits (O’Connor 1997). Some even contend that domesticates manipulated unwitting humans into relationships that gave the domesticate great evolutionary advantage at the expense of human fitness (Rindos 1984, Budiansky 1992, Morey 1994).

I take a more centrist position. I acknowledge that both partners in the domestic relationship reap benefits through their increasing reliance on each other. In this way domestication is indeed quite similar to mutualistic relationships in the natural world like those between farmer ants and “domesticated” fungi or between other ant species and their aphid “herds”, the most commonly cited analogies with human plant and animal domestication (Rindos 1984). But the mutualism that lies at the heart of the domestication process differs from these convergent forms of biological mutualism in one important and uniquely human way (Schultz *et al.* 2005, Zeder 2006a, 2009). Mutualistic relationships in nature are the product of extended evolutionary processes driven by selection operating on mutation-induced variation in behavior and morphology *in both partners*, with adaptive changes in behavior and body form passed on to future generations through genetic transmission in the course of sexual reproduction. The co-evolutionary relationships between humans and target domesticates, on the other hand, are largely driven by the human ability to spontaneously invent new behaviors that maximize the return of a desired plant or animal resource and, most importantly, to pass on behaviors that best meet these goals to their offspring and to others through social learning. This capacity for the cultural transmission of learned behavior ramps up the mutualism between humans and emerging domesticates and transforms it beyond anything seen in nature. Both partners still derive mutual benefit, plants and animal partners vastly enhance their reproductive fitness and humans gain a predictable and secure resource base. But the human capacity for social learning puts humans in a dominant role in an increasingly asymmetrical mutualism that moves at a vastly accelerated pace and carries a much broader impact than any such relationship in nature.

The process of domestication unfolds across multiple axes on both the plant/animal and human sides of the equation (Figure 9.1). A primary axis on the plant/animal side involves the phenotypic expression of genetic changes that transforms the plant or animal from its wild phenotype to its domestic phenotype. Progress along this axis is driven by a number of selective and random processes that operate either sequentially or in tandem depending on the domesticate and the nature of its relationship to its human partners (see Price 1984, 1999, 2002). Human-orchestrated directed, or artificial, selection for desired traits is only one of the forces that shape a domesticate’s trajectory along this axis. Other forces may play an even more important role in shaping the domestic phenotype,

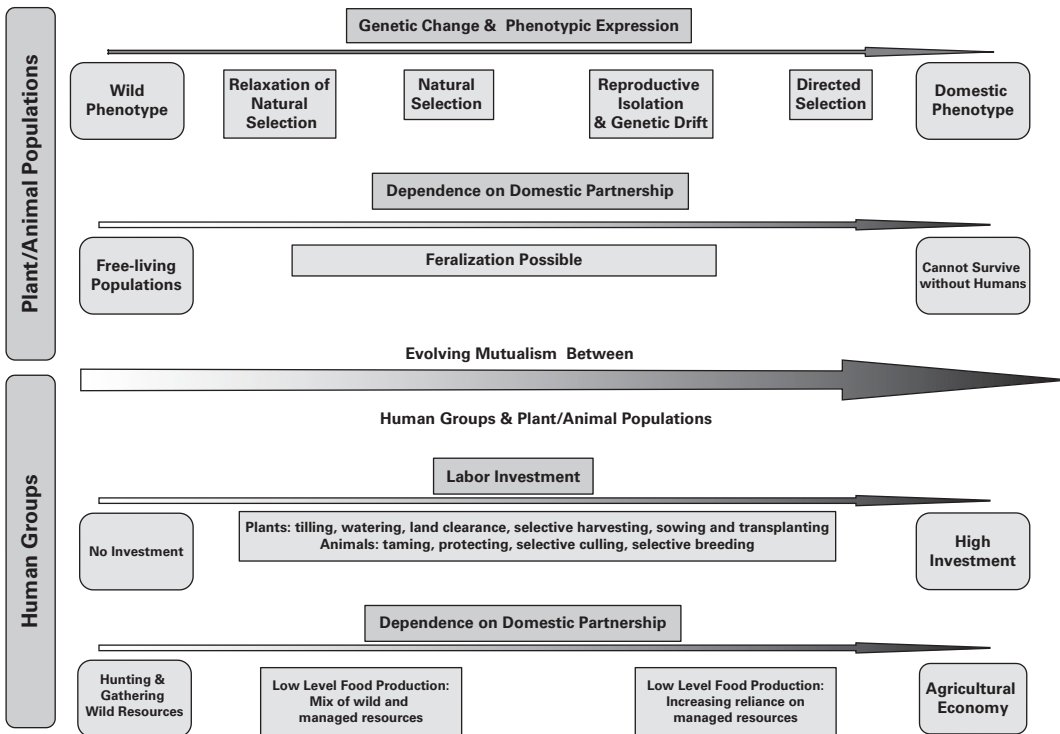


Figure 9.1. Multiple axes of domestication.

especially early on in the domestication process. These include both the relaxation of natural selection once the plant or animal comes under human control and the adaptation to the new selective pressures on the plant or animal as it enters a human environment. Random forces also play a role when, often through human-mitigated movement, small populations of plants and animals are isolated from broader breeding pools, creating “founder” populations that carry a small, more or less random selection of the much broader range of genetic variation of the progenitor population. Another axis on the plant/animal side of the partnership involves their increasing dependence of the domesticate on the relationship with humans. Movement along this axis ranges from free-living populations, to managed ones which can still revert to a wild state, to plants and animals unable to survive outside of the domestic partnership.

The degree of human investment in the plant or animal species forms an important axis on the human side of the domestic partnership. This axis moves from no investment (either because humans ignore the plant or animal entirely or do not engage in any effort to manipulate its availability), to a wide range of increasingly intensive activities aimed at encouraging the supply of a desired plant or animal resource. These behaviors may involve altering the plant or animal’s environment, providing nourishment and protection from predation,

or intervening into its reproductive cycle (Harris 1996, Smith 2007a, b). Increasing human dependence on the plant or animal forms another axis on this side of the relationship. In this case, humans move from complete dependence on free-living populations, through various levels of what has been termed “low-level food production” based on a mix of managed and free-living resources, to an agricultural economy in which domesticates make up 40%–60% of human caloric intake (Smith 2001).

All these different axes operate simultaneously during the domestication process. And while every instance of plant or animal domestication involves movement along these axes, not all domesticates travel across these axes at the same pace or direction. Pathways to domestication vary depending on a range of morphological, physiological, and behavioral constraints in the target domesticate, the intensity of human investment, the importance of the resource in the human subsistence economy, and the overall environmental context within which the relationship unfolds. The challenge to those studying domestication, whether in plants or in animals, is to identify ways to trace the variable pathways to domestication and identify the forces that direct humans and domestic partners along these pathways, in the past and the present and into the future.

2 Basics of animal domestication

Although similar co-evolutionary processes drive the domestication of both plants and animals, there are fundamental differences between plants and animals that determine which taxa enter into domestic partnerships with humans and how they respond to the domestication process once underway. Characteristics that make certain plants attractive candidates for domestication center on morphological attributes (i.e., the possession of edible fruits, seeds, or underground storage organs) or growing habits (i.e., a generalized ability to colonize and adapt to open, disturbed habitats). Responses to the ongoing domestication process in plants may take the form of alterations in germination or dispersal mechanisms as plants adapt to the human-mitigated ecosystems, loss of various defenses against herbivory due to the relaxation of selective pressures for defense once humans start tending plants, or changes in fruit size, starch content, and sugar content that may arise as the result of deliberate human selection for desired traits. (Smith 2006).

In animals, on the other hand, candidacy for domestication, the targets of selection under domestication, and the responses to domestication center almost exclusively on behavioral characteristics (Hale 1969, Clutton-Brock 1981, Price 1984, 2002). Physiological and morphological responses to these pressures in animal domesticates are often secondary artifacts of the intense selection on animal behavior (Zeder 2006b). Identifying the behaviors selected for under domestication and the impact of this selection on domestic animals is, then, essential for understanding animal domestication.

Favorable Characteristics	Unfavorable Characteristics
1. Social Structure a) Large gregarious social groups b) Hierarchical group structure c) Males affiliated with social group 2. Sexual Behavior a) Promiscuous mating system b) Males dominant over females c) Sexual signals provided by movement or posture 3. Parent-Young Interactions. a) Social bonds created through imprinting b) Female accepts young soon after parturition or hatching c) Precocial young 4. Responses to Humans. a) Short flight distance away from humans b) Low reactivity to humans or sudden changes in environment c) May solicit attention d) Readily habituated 5. Feeding Behavior & Habitat Choice a) Generalist feeder or omnivorous b) Wide environmental tolerance c) Non-shelter seeking	1. Social Structure a) Family groupings b) Territorial structure c) Males in separate groups 2. Sexual Behavior a) Monogamous mating system b) Females dominate males/males appease females c) Sexual signals provided by markings or morphology 3. Parent-Young Interactions a) Social bonds created on basis of species characteristics b) Female accepts young on basis of species characteristics c) Altricial young 4. Responses to Humans a) Extreme wariness and long flight distance b) Easily disturbed by humans or sudden changes in environment c) Independent/avoids attention d) Difficult to habituate 5. Feeding Behavior & Habitat Choice a) Specialized dietary preferences or requirements b) Narrow environmental tolerance c) Shelter seeking

Figure 9.2. Pre-adaptive behavioral characteristics in animal domestication. From Hale 1969, Price 1984, 2002.

2.1

Behavioral characteristics in domestic animals

Attributes thought to be “pre-adaptive” to domestication in animals can be grouped under five general categories of behaviors that affect (1) Group structure, (2) Sexual behavior, (3) Parent–young interactions, (4) Responses to humans, and (5) Flexibility (Figure 9.2), (Hale 1969, Price 1984, 2002). Many of these behaviors make it possible for humans to insert themselves in the animal community – either co-opting leadership of group structure, determining breeding partners and reproductive timing, or assuming a parenting role over young animals soon after birth. Behaviors that affect an animal’s response to humans are also critical, with those that determine flight distances and reactivity to external stimuli especially important in this regard. Other pre-adaptive attributes include behaviors that afford the animal more flexibility in meeting dietary and other environmental requirements for survival. In general, the degree to which a species is pre-adapted to domestication is positively correlated with the degree to which its behavior in its natural environment resembles its behavior in its captive environment. Species with the fewest behavioral pre-adaptations to domestication are either never considered as potential domestic partners or, when domesticated, experience the most extensive changes in response to the selective pressures of the domestication process (Price 2002:22).

Once animals embark on the pathway to a domestic partnership with humans, the primary target of the new selective pressures introduced by this developing relationship are those that determine the animal’s response to humans and the

human environment. In all domesticated animals, the single most important behavioral response to domestication is reduced wariness and low reactivity to external stimuli (Price 1998:51–2, 2002:18). This is true of all orders of domesticated mammals, including carnivores (Trut 1999, Coppinger and Coppinger 2001), herbivores (Tennessen and Hudson 1981), and rodents (Murphy 1985), as well as domestic birds (Andersson *et al.* 2001) and fish (Waples 1991), and even domesticated invertebrate species (Marliave *et al.* 1993, Price 2002:27–9). And it is the selection for reduced wariness and low reactivity that has the most profound and most universal impact on domestic animals.

2.2 Brains and behavior

The most significant impact of this intense selection for reduced wariness and low reactivity to external stimuli is seen in the size, organization, and function of the brains of domesticated animals. Numerous studies have noted a systematic reduction in the overall size of brains in domestic animals compared with their wild progenitors (Figure 9.3), (Kruska 1988, 1996, Plogmann and Kruska 1990, Ebinger 1995, Ebinger and Röhrs 1995). Within broad classes of domesticated mammals, there is a positive correlation between the degree of encephalization (brain mass above that related to an animal's body mass) and brain size reduction. Mammals with larger brains seem to have experienced the greatest degree of brain size reduction, whereas smaller-brained mammals may experience little or no overall reduction in brain size with domestication (Kruska 1988:217, Figure 9.3). Pigs (*Sus scrofa*) seem to have undergone the greatest degree of brain size reduction of any domesticate (33.6%), followed by various domesticated carnivores in which brain size reduction varies between 20% and 30%. Brain size reduction in domesticated ungulate species ranges from 14% to 24%, while domesticated rodents show the smallest degree of brain size reduction. This same relationship generally holds true among domesticated birds (Röhrs 1985, Ebinger 1995), with the exception of domestic turkeys (*Meleagris gallopavo*) which show a large, almost 30%, reduction in brain size compared with their relatively small-brained wild counterpart – although this large difference may result from the comparison of a possibly non-ancestral wild subspecies with a highly improved modern breed of turkey (Ebinger and Röhrs 1995). Even captive-reared fish like rainbow trout (*Oncorhynchus mykiss*) show significant reduction in brain size compared with wild trout, especially in the areas of the brain linked to aggression, feeding behavior, and reproduction (Marchetti and Nevitt 2003).

The degree of brain size reduction does not seem to be positively correlated with the length of time since original domestication. Sheep (*Ovis aries*), domesticated more than 10,000 years ago, display a 24% reduction in brain size compared with ancestral species (*Ovis orientalis*), whereas ferrets (*Mustela furo*), domesticated for only 2,500 years, show a 30% brain size reduction compared with wild polecats

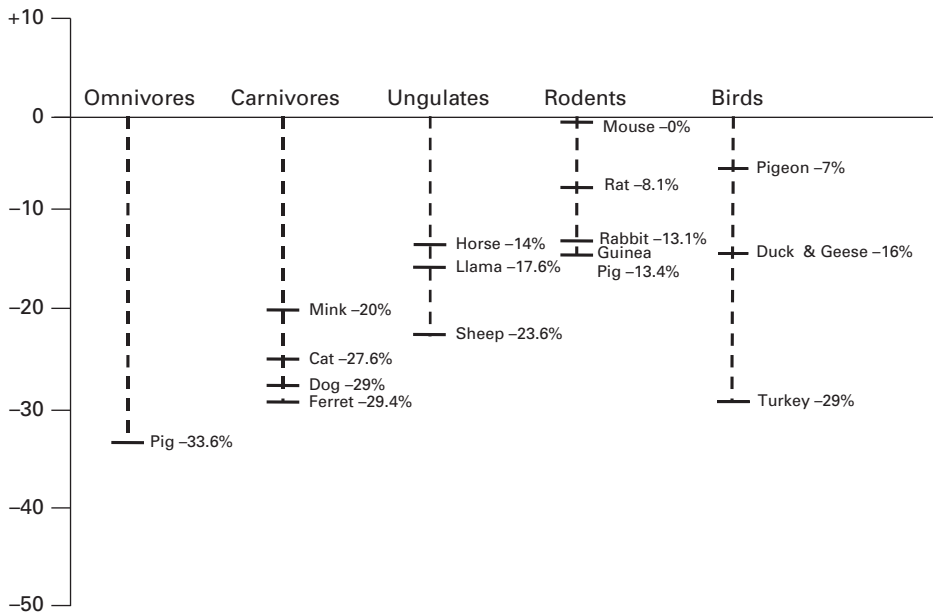


Figure 9.3. Reduction in brain size in different groups of domestic animals. Shown as the percentage of brain mass (corrected for body mass) loss compared to wild ancestral species at comparable body mass. From Kruska 1988, 1996, Ebinger 1995, Ebinger and Röhrs 1995, Rehkämper *et al.* 2008.

(*M. putorius*). Cage-reared ranch mink (*M. vison*) have experienced a 20% reduction in brain size since they were brought under domestication a little over 100 years ago (Kruska 1996). Silver foxes (*Urocyon cinereoargenteus*) selectively bred for tameness experienced a reduction in cranial height and width, and by inference in brain size, after only 40 years of intensive breeding (Trut 1999). It seems likely, then, that reduction of brain size in animals undergoing domestication may have occurred relatively quickly during the early phases of the domestication process and is directly linked to selection for reduced wariness and low reactivity to humans.

Not all parts of the brain are equally affected by the selective pressures introduced by domestication, and there are species-specific differences in the degree of size reduction in different parts of the brain in both domestic mammals (Figures 9.4 and 9.5; Kruska 1988, 1996, Plogmann and Kruska 1990) and in domestic birds (Ebinger 1995, Ebinger and Röhrs 1995). In pigs, for example, brain parts involved in the processing of auditory and olfactory stimuli are less reduced than visual structures, leading Plogmann and Kruska (1990) to conclude that structures controlling critical functions in the ancestral species may be less affected by domestication-induced brain size reduction than less critical functions. Although the telencephalon, which controls higher thought processes and sensory perception, is the region of the brain most profoundly reduced in most domestic mammals, in domestic mink the mesencephalon and the cerebellum, which control

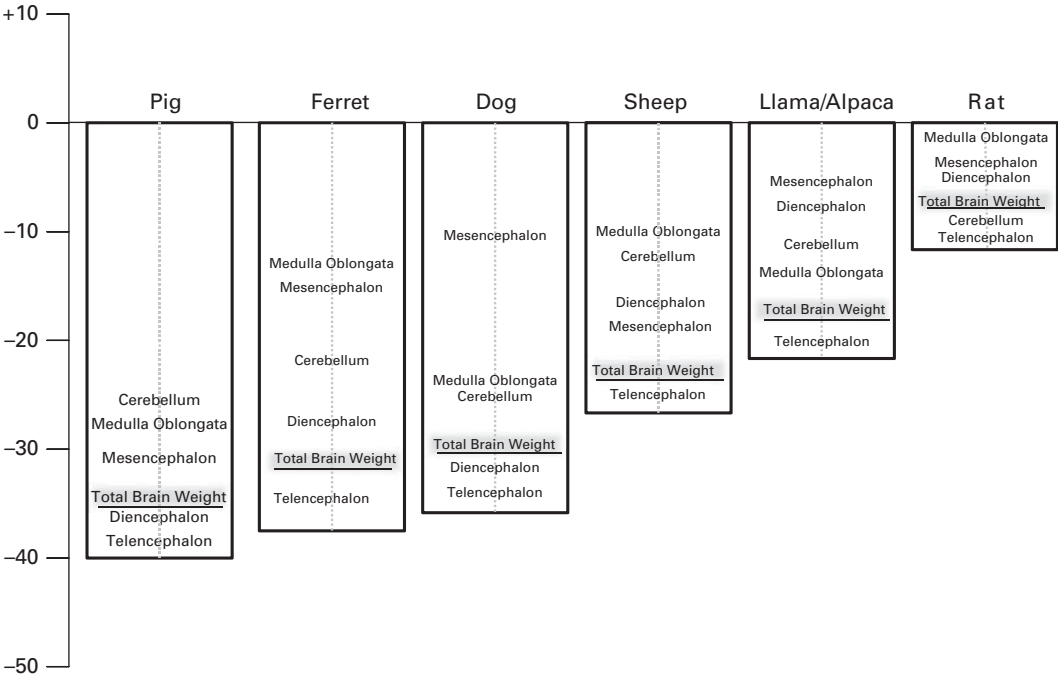


Figure 9.4. Reduction in total brain mass and size of fundamental brain structures in several species of domestic animals. Shown as the percentage of brain mass (corrected for body mass) loss compared to wild ancestral species at comparable body mass. From Kruska 1988.

body movements, show the greatest degree of size reduction – an adaptation, it is proposed, to the spatial restrictions of cage rearing in this highly active mustelid species (Kruska 1996). It is interesting to note in this regard that ranch mink kept in cages have experienced a much more significant overall reduction in brain size (20%) than mink raised in open-air enclosures, in which brain size is only 11% smaller than in wild mink (Kruska 1988, 1996, Price 2002:87). Not all brain size changes in domestic animals are in the direction of smaller size, however. Although net brain volume is reduced in domestic pigeons (*Columba livia*) compared to wild rock doves, the hippocampus, important in memory and learning, is larger, especially among racing and homing pigeons – a likely functional adaptation to homing that requires spatial cognition and sensory integration (Rehkämper *et al.* 2008). As a general rule, phylogenetically younger parts of the brain are more profoundly affected than are “older” structures (Kruska 1988:219). This general pattern is seen by some animal scientists as evidence of “regressive evolution” in domestic animals (Röhrs 1985:547). Others, however, suggest that these structures change more because they are more plastic than more basal brain structures and therefore more responsive to the relaxed need for higher-level brain functioning once humans become buffers between the animal and its environment (Price 2002:89).

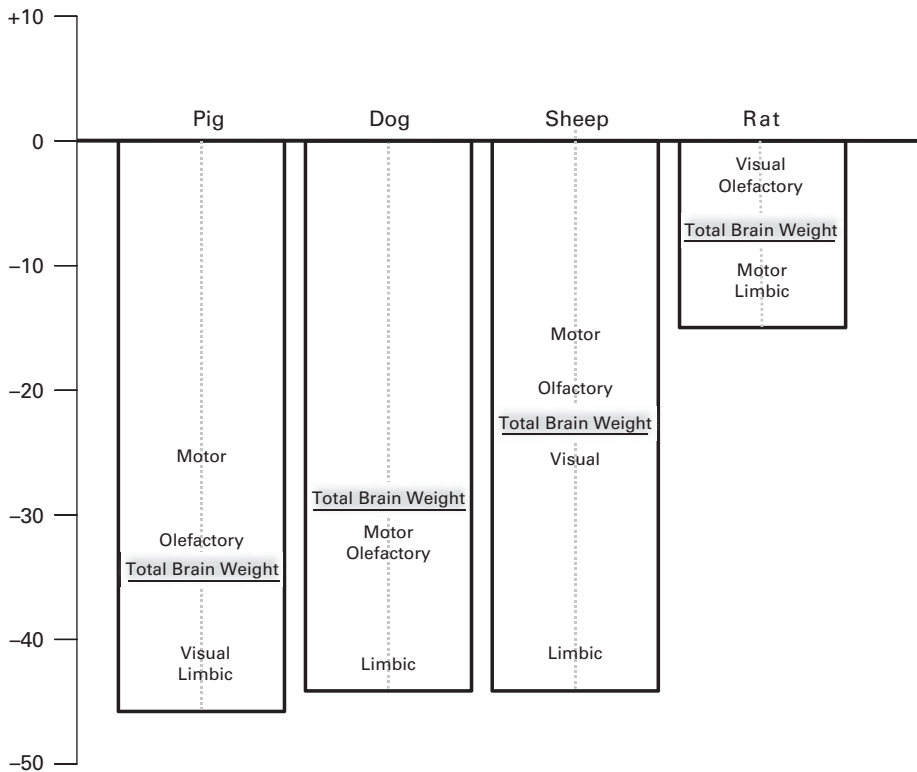


Figure 9.5. Reduction in the volume of brain structures in different functional systems in several species of domestic animals. Shown as the percentage of brain mass (corrected for body mass) loss compared to wild ancestral species at comparable body mass. From Kruska 1988.

The proposed correlation between the degree of reduction and phylogenetic age of brain structures is undercut somewhat by the fact that the region of the telencephalon most profoundly affected by domestication in highly domesticated animals, such as dogs, sheep, and pigs, is the complex set of structures that belong to the limbic system, which are embryologically, and likely phylogenetically, some of the oldest parts of the brain (Figure 9.5). Comprising the hippocampus, the hypothalamus, the pituitary gland, and the amygdala, the limbic system is responsible for controlling emotionally guided behaviors and memory. It operates by influencing the endocrine and the automatic nervous systems that directly control an animal's responses to threats and other external stimuli. The profound reduction in the size of structures within the limbic system in domestic animals can, then, be directly tied to raising the behavioral thresholds for the display of such behaviors as aggression, fear, and flight resulting in an overall reduction of emotional reactivity that is the keystone behavioral attribute of domestic animals (Kruska 1988:221, Price 2002:89).

The linkage between behavior, endocrine function, and domestication is powerfully demonstrated by the work of Künzl and colleagues, which compares behavior and endocrine function in domestic guinea pigs (*Cavia porcellus*) and wild cavies (*Cavia aperea*) (Künzl and Sachser 1999, 2000, Künzl *et al.* 2003). When compared with wild-trapped cavies and their first-generation offspring, domestic guinea pigs show significantly less aggressive behaviors and more socio-positive behaviors toward conspecifics. They are also less attentive to their surroundings, but are more likely to engage in courtship and sexual behaviors. The endocrine responses of wild and domestic cavies are also significantly different. Wild cavies subjected to stressful situations (handling and placement in an unfamiliar cage) register much higher responses in both the pituitary–adrenocortical (PAC) and the sympathetic–adrenomedullary (SAM) systems, major endocrine stress axes that under conditions of long-term hyper-activation can contribute to an animal’s injury or death. At the same time, serum testosterone levels in domestic males are significantly higher than in their wild counterparts, a factor no doubt contributing to the greater degree of courtship behavior seen among domestic males. The correlation between higher stress and lower courtship thresholds in domestic guinea pigs reinforces the notion that, rather than having undergone regressive evolution, domestic animals have developed highly successful adaptations to captive environments. Interestingly, captive wild cavies reared in captivity for 30 generations without selective breeding for tameness were found to exhibit the same behavioral and endocrine responses as wild-trapped cavies, suggesting that it takes more than simple captivity to bring about the attenuation of emotional reactivity found in domestic animals (Künzl *et al.* 2003). This finding is reinforced by studies that report similar differences in brain chemistry in silver foxes bred for tameness (Popova *et al.* 1991a) and in Norway rats (*Rattus norvegicus*) selected for reduced aggression to humans (Naumenko *et al.* 1989, Popova *et al.* 1991b).

2.3 Pleiotropic effects of selection for behavioral attributes

Selection for reduced wariness and low reactivity may be pleiotropically linked to other behavioral, physiological, and morphological features commonly found in domestic animals (Price 2002:79). Among these traits are those that relate to alterations in developmental events, or heterochrony, especially a reduction in the rate of change in development known as paedomorphosis. One form of paedomorphosis commonly found in domestic animals is neoteny, in which an animal passes through fewer developmental stages before it reaches adulthood so that as an adult the animal resembles a juvenile stage of its ancestor (Goodwin *et al.* 1997). Neoteny may be manifested in the early onset of sexual maturity or in the retention of both juvenile behaviors and morphology, especially the retention of juvenile cranial morphology. The classic example of domesticates thought to display all these neotenized features is the dog (Coppinger *et al.* 1987, Coppinger and Schneider 1995, Fox 1978, Goodwin *et al.* 1997, Morey 1994). Other

pleiotropically linked effects of selection for reduced aggression may be found in coat color, especially the manifestation of white markings or piebald coloration, with a connection drawn between the melanins involved in coat coloration and the biochemical pathways traveled by neurotransmitters like dopamine that play a role in shaping behavior and cognition (Hemmer 1990:121–30, see also Keeler *et al.* 1968). Features like lop ears and shortened or curled tails, which arise relatively quickly in foxes bred for tameness, may also be part of a linked complex of domestic traits (Trut 1999).

Recent work on gene expression provides a possible explanation for the pleiotropic linkage of seeming disparate behavioral, physiological, and morphological traits in domestic animals. Qualitative-trait-locus (QTL) analysis of second-generation crosses between jungle fowl (*Gallus gallus*) and white leghorn chickens (*Gallus domesticus*) successfully identified loci containing alleles that differentially affect the expression of the phenotypic traits (i.e., egg production, growth rates, plumage coloration, fearfulness, and aggression) (Jensen 2006). Specifically, several of the QTLs responsible for various productive traits were closely linked with QTLs for behavior. Extrapolating from these results, the author of this study suggests that the pleiotropic cascade of traits observed in domestic animals may be caused by mutations in regulatory genes responsible for the orchestration of gene expression during development. Under such a scenario only a handful of mutations in regulatory genes are needed to account for major and rapid evolutionary changes that separate wild from domestic animals. If so, the intense selection for certain behavioral attributes of animals embarking on a domestic partnership with humans could be responsible for a suite of other behavioral, physiological, and morphological changes in domestic animals.

2.4 The imprint of domestication

The lasting impact of the changes associated with domestication in animals can be clearly seen in feral animals that have left the domestic relationship and have reverted to living in a wild state. Sometimes referred to as a process of domestication in reverse, feralization is often looked to as a model for understanding the nature and permanence of the changes associated with domestication (Letts 1964, Hale 1969, Brisbin 1974, Price 1984, 1999, 2002).

Domestication-induced changes in brain size and function may well be irreversible. Feral dogs, cats, goats, donkeys, and ferrets that have lived outside of a direct association with humans for many generations show no sign of regaining the brain mass (Herre and Röhrs 1990, Birks and Kitchener 1999). Wild mouflon (*Ovis orientalis musimon*) on Mediterranean islands that a combination of morphological, cytological and genetic studies confirm are the feralized descendents of the domestic stock of Neolithic colonizers (Nadler *et al.* 1973, Poplin *et al.* 1986, Bruford and Townsend 2006) retain the smaller brain size of their domestic ancestors even though they look in every other regard like wild sheep (Groves

1989). Dingos (*Canis familiaris dingo*) in Australia and New Guinea, which have been living outside of a domestic relationship for thousands of years, have the same brain size as domestic dogs (Schultz 1969).

A study of feral pigs in the Galapagos found that although there was some evidence of a reversal of the effects of domestication in certain attributes, other attributes remained unchanged (Kruska and Röhrs 1974). Over the approximately 150 years since these animals were introduced onto the islands they have regained some of the body structure of European wild boar (i.e., longer legs and snouts), but still retain the coloration of domestic pigs. An examination of the brains of four of these feral animals found some increase in size of structures related to olfaction, and the size of the hippocampus may have increased slightly, although it still remained at least 30% smaller than in wild boar. The brains of feral Galapagos pigs also exhibited a greater degree of variability in the size of the limbic center. A similar degree of variability in the size of this region of the brain is also seen in wild pigs, but not in domestic swine. Kruska and Röhrs suggest that the greater degree of variability in the size of limbic structures in the Galapagos pigs might be linked to an increase in aggression and reactivity among these animals, which, though they lack natural predators on the Galapagos, have been intensively hunted by humans. However, these feral pigs showed no signs of overall brain size increase, nor was there any detectable increase in the size of the telencephalon, the region of the brain generally most significantly affected by domestication-induced brain size decrease.

The domestic imprint is also quite evident in the behaviors of feral animals. Feeding habits of feral domestic cats (*Felis catus*) in Hungary are quite generalized and include a relatively wide range of small animals, especially terrestrial mammals (Bíró *et al.* 2005). Hungarian European wild cats (*Felis silvestris*), on the other hand, specialize to a greater degree on particular small mammal species. They also consume a much higher proportion of arboreal prey that includes both small perching birds and some larger birds like pheasant and woodcock, suggesting that wild cats had more hunting prowess than feral cats. Studies of feral and wild cats in Scotland (Corbett 1979) and Iberia (Gil-Sánchez *et al.* 1999) lend support to this conclusion. Where rabbit (*Oryctolagus cuniculus*) populations are large, wild cats predate them heavily. Feral cats, in contrast, only occasionally consume rabbits in quantity and when they do they focus mainly on juvenile or sick individuals. Moreover, although the Hungarian feral cats are much less likely to consume household foods than scavenging domestic cats, they nevertheless derive one-fifth of their prey from human settlements (Bíró *et al.* 2005). Wild cats in this study took no prey from human settlements. Free-ranging cats and dogs in southeastern Brazil are found in significantly higher density in suburban areas than in rural ones, suggesting that these animals retain a strong connection to the human environment and are not exploiting more open niches in rural areas to the same extent (Campos *et al.* 2007).

In a broad-ranging synthesis of the literature on the social ecology of feral dogs (*Canis familiaris*), Boitani and Cuicci (1995) conclude that even fully feralized

animals, which receive no food or shelter from humans and show a strong avoidance of human contact, are still dependent on the human niche for survival and have not regained the self-sustaining behaviors found in wolves (*Canis lupus*). Whereas wolves live in single family packs with established hierarchical social structure, feral dogs live in fluid groups made up of breeding pairs. The size of these groups is limited by the lack of social structure and other social bonds that keep wolf packs operating as functional units. Although feral dogs generally have larger litters and breed more frequently than wolves, they lack the parenting skills of wolves, often leaving very young pups unattended, resulting in high juvenile mortality. Older feral pups also suffer higher mortality rates than wolf pups of comparable age when they leave the den to explore and forage on their own or when their mother enters a new oestrous cycle and loses interest in her most recent litter. As a result, groups of feral dogs are not self-sustaining and can only be maintained through recruitment of new members from populations of stray dogs. Feral dogs do not hunt in packs like wolves and, again unlike wolves, feral pups are not taught to hunt by adult animals. As a result these dogs have a highly diversified diet comprising primarily smaller, easier to catch prey. Although they may not receive food directly from humans, they still concentrate on human-mitigated landscapes when foraging for food.

Thus the imprint of domestication on animals is profound. Domestication-induced changes in brain size and function are deep-rooted and perhaps irreversible. Behavioral attributes selected for during domestication make it difficult, if not impossible, to recapture the behaviors and social ecology that sustained their progenitors in the wild. Feral animals attempting to divorce themselves from the domestic partnership with humans seem only partly successful in doing so and in many ways remain strongly tied to humans, even if indirectly.

3 Pathways to domestication

There seem, then, to be universal attributes found in almost all domestic animals in the behaviors selected for under domestication and the impact of this selection on brain form and function. But did all domestic animals acquire these attributes in the same way? Did all animal domesticates travel the same general pathway that took them from free-living wild animals to animals forever tethered to a partnership with humans, even when they attempt to revert to the wild state? I think that there is ample evidence that this is not the case and that even though there are universal attributes found in all animal domesticates, the pathways to animal domestication were highly variable and contingent on broadly defined biological and cultural parameters, as well as a range of highly localized factors that shaped the trajectories of individual cases of animal domestication (Zeder 2009). These varied pathways can, however, be grouped into three general domestication scenarios that seem to account for the full spectrum of animal domesticates – a commensal pathway, a prey pathway, and a directed pathway (Figure 9.6).

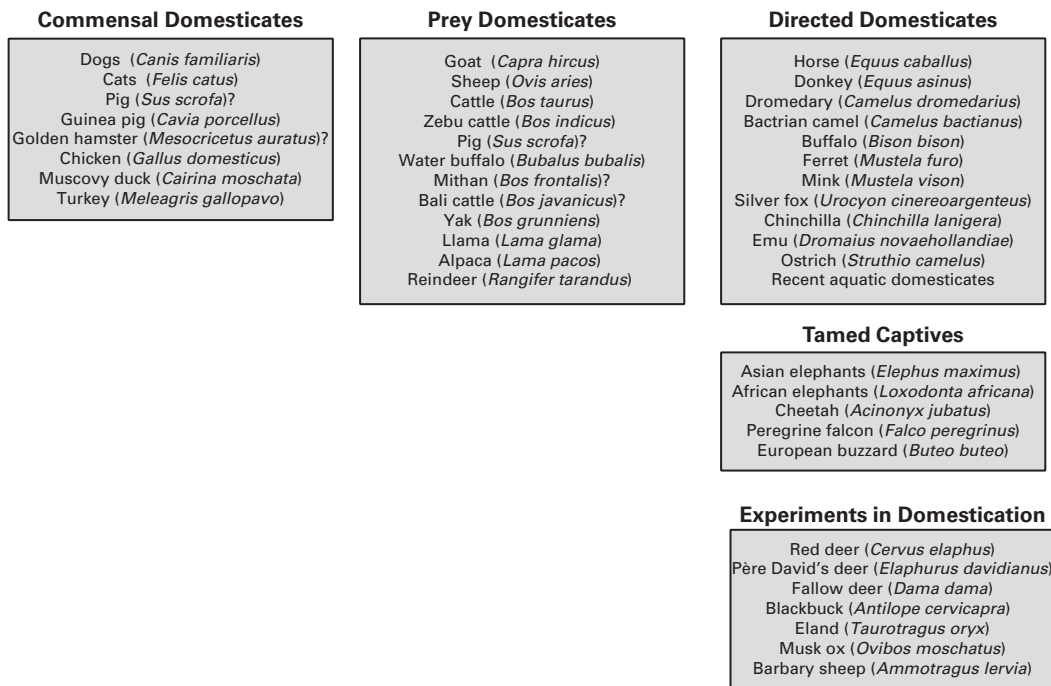


Figure 9.6. Possible pathways to domestication of animal species mentioned in the text.

3.1 Commensal pathway

The first of these pathways, the commensal pathway, is most frequently traveled by animals that come into initial contact with humans to feed on refuse or to prey on other animals attracted to human settlements. At some point in their association with humans and human habitats, these animals developed closer social or economic bonds with their human hosts than did other commensals inhabiting this niche. These bonds brought them, eventually, into a domestic partnership with humans. The classic example of an animal that likely traveled this pathway to domestication is the dog, whose domestication is thought to have begun when less wary wolves were drawn to human encampments to scavenge on human refuse (Coppinger and Coppinger 2001, Morey 1994). In a comparative study of the skeletal morphology of wolves and dogs, Morey (1992) concludes that the principal difference between the dog and its wild progenitor lies in the juvenilization of the adult dog's cranial morphology, which resembles that of a juvenile wolf in its shorter face, steeped forehead, and wider cranial dimensions. Morey suggests that these differences in cranial morphology are artifacts of neotenization arising out of a general process of paedomorphism in developmental rates (see also Trut 1999, but see Wayne 1986, who contends that dog and wolf skulls differ primarily in cranial width, which is not a paedomorphic trait). The mandibles of dogs are shorter than those of wolves and there is

considerable reduction in the length of their molars (Wayne 1986). These features are found in even the earliest examples of domestic dogs like the 13,000-year-old mandible recovered from Palegawra Cave in northeastern Iraq, which shows clear evidence of tooth size reduction and crowding in a shortened jaw (Turnbull and Reed 1974). The dogs buried with humans at the roughly contemporary site of Ain Mallaha in the southern Levant also display these traits, and their occurrence in burial contexts speaks to the strong social bonds that had been forged between dogs and humans at this early date (Davis and Valla 1978, Tchernov and Valla 1997, Morey 2005). This same site also contains some of the earliest remains of commensal animals like the house mouse (*Mus musculus*), the spiny rat (*Echimyus chrysurus*), and the house sparrow (*Passer domesticus*) (Tchernov 1991), species that traveled a commensal pathway into close association with humans but that, unlike dogs, did not complete the journey to domestication. Recent genetic data support archaeological evidence that suggests initial dog domestication took place in the Near East (vonHoldt *et al.* 2009).

A surprising number of common domestic animals may have traveled this same pathway to domestication. Archaeological evidence pushes back the date of cat domestication to at least 8,500 years ago (Vigne *et al.* 2004), and new genetic evidence points to a Near Eastern origin for initial cat domestication (Driscoll *et al.* 2007). It is likely, then, that cats, like dogs, were drawn into initial contact with humans when humans began to live in more permanent settlements and these obligate carnivores were attracted to human habitats to prey on other small commensal species occupying this niche. Interestingly, however, cats did not experience similar changes in cranial morphology, nor does the social ecology of these more solitary animals seem as profoundly altered by domestication.

Chickens, which genetic evidence suggests were domesticated multiple times in southeast Asia, China, and perhaps India (Liu *et al.* 2006, Kanginakudru *et al.* 2008), may also have entered the domestic relationship with humans through a commensal pathway as wild jungle fowl sought out human dump heaps for easy sources of grain. A similar pathway might be suggested for the domestication of the turkey in the southwestern US (Munro 2011). Muscovy ducks (*Cairina moschata*) in Amazonia have been argued to played an important role in reducing insect populations in human settlements (Angulo 1998), an outgrowth, perhaps of a similar initial commensal introduction into the human sphere. Another likely commensal domesticate is the guinea pig (*Cavia porcellus*), first domesticated in the highland Andes around 7,000 years ago (Spotorno *et al.* 2006). Golden hamsters (*Mesocricetus auratus*), which are indigenous to Syria, Israel, and eastern Turkey and known for the ease with which they can be handled in the wild, are another candidate for a commensal domesticate – although the hamsters kept so widely today as pets and laboratory animals are thought to be descendants of a quite recent and deliberate domestication of hamsters from dwindling wild populations (Murphy 1985).

It is also possible that pigs, a major livestock species, entered into domestication through a commensal pathway. Archaeological evidence from the site of Hallan Çemi in southeastern Anatolia suggests that, as with dogs and cats, a special

relationship between pigs and humans began as early as about 12,000 calendar years ago, soon after humans began living in more established year-round settlements (Redding 2005). There are multiple lines of evidence for the intensification of this relationship over the course of nearly 3,000 years of occupation (from 10,500 to 8,300 cal BP) at the near by site of Çayönü (Ervynck *et al.* 2001, Hongo *et al.* 2002). As with dogs, the leading edge indicator of pig domestication is a gradual reduction in molar length, a marker of domestication in pigs thought to result from the neotenization of skull morphology (Flannery 1983). These gradual changes in tooth morphology are first detected several hundred to a thousand years prior to the appearance of other markers of pig domestication at this site. Ervynck *et al.* (2001) see this long lead-up period as evidence of an evolving mutualism between pigs and humans initiated by wild pigs originally drawn to human settlements to scavenge off refuse dumps.

3.2 Prey pathway

Most major livestock species, however, entered into domestication through what might be called a prey pathway. Rather than initiating the relationship, these animals were primary prey species that humans had hunted for their meat and hides for thousands of years. The prey pathway likely began when, perhaps as a response to depletion of local stocks of these prey animals, humans developed hunting strategies designed to increase prey availability. Over time and under certain circumstances, these game management strategies developed into actual herd management and, eventually, the controlled breeding of managed animals.

Archaeological evidence from the Near East suggests that sheep (*Ovis aries*), goats (*Capra hircus*), and cattle (*Bos taurus*) all followed this pathway to domestication, with the transition from generalized hunting to specialized hunting and then herd management taking place within the natural habitats of wild progenitor species (Zeder 2008a, 2009, 2011). This process seems to have unfolded over many hundreds, if not thousands, of years without any clear-cut, archaeologically detectable morphological changes in the animals traveling down this pathway to domestication. These early stages of the transition from hunting to initial management may only be detectable in the demographic profiles of the animals harvested by humans, especially in the separate harvest patterns of male and female animals. Constructed using the fusion patterns of post-cranial skeletal elements, these sex-specific harvest profiles are capable of distinguishing between the prey strategies of hunters that seek to maximize immediate meat return (often reflected by an emphasis on large adult males) from those of herders directed at promoting herd growth (most commonly met by the early harvest of all but a few males and the delayed cull of older females past peak reproductive years) (Zeder 2006b, 2008b). This distinctive herd management harvest profile is first detected in goat assemblages from the archaeological site of Ganj Dareh in the Central Zagros Mountains of modern-day Iran at about 10,000 calendar years ago (Zeder and Hesse 2000, Zeder 2006b, 2008b). Lower-resolution harvest data collected by

using other methods, however, suggest that the management of both sheep and goats began perhaps 500 to 1,000 years earlier in the highland regions of the eastern Taurus and northwestern Zagros Mountains (Peters *et al.* 2005, Zeder 2008a, 2009, 2011). The initial phases of the transition from hunting to herding in this region may also reach back to about 12,000 to 13,000 calendar years ago. New demographic data from southeastern Turkey and northwestern Iraq point to the development of hunting strategies, which may have helped restock local herds of wild sheep depleted by people living in increasingly sedentary settlements (Redding 2005, Zeder 2008b, 2009). Demographic data for cattle suggest that a similar process was underway in the upper Euphrates Valley by about 10,500 to 10,000 years ago (Helmer *et al.* 2005).

A recent genetic analysis by Naderi *et al.* (2008) has identified all six domestic goat lineages among modern wild bezoar goats from eastern Turkey and western Iran. The authors of the study argue that the presence of these domestic haplogroups among wild goats is not an artifact of recent introgression between domestic and wild goats. They maintain instead that genetic signatures of population growth and geographic translocation represent residual evidence of initial human domestication of these different lineages and the human-mitigated movement of managed animals within and out of this heartland region of initial domestication. This exciting new study suggests that although the prolonged periods of human management of goats within their natural habitat had no detectable morphological impact on these animals, it nevertheless left a genetic imprint observable even today among the descendant populations of wild goats from which domestic lineages were originally drawn.

Domestication-induced morphological change in animals traveling along this prey pathway may only be detectable once humans took managed herds out of the natural habitat of their wild progenitors where factors like genetic drift and adaptation to new environments came into play. The movement of managed herds outside of the range of wild populations also eliminated the chance of introgression between wild and managed animals or the possibility of restocking managed herds with wild animals – both probably quite common occurrences in the initial phases of herd management. Once this link was cut in managed sheep and goats, we begin to see distinctive changes in horn size and shape like those evidenced at about 9,500 to 9,000 cal. BP among the remains of goats recovered from the archaeological site of Ali Kosh in lowland Iran (Zeder 2006b). Changes in the size and shape of horns of domesticated ungulates like sheep, goat, and cattle likely arose from a combination of factors including: (1) the relaxation of selective pressures for large horns previously used to both attract and compete for females, (2) the expression of random mutations previously selected against when horns were used in mate competition, (3) the impact of new selective pressures against energetically expensive and no-longer-needed horn architecture, and (4) directed human selection for more tractable males.

These same factors likely also played a role in changes in body size in these early domestic livestock species. However, rather than an overall reduction in the body

size of initial domesticates as was once thought to be the case (Uerpmann 1979, Meadow 1989), it now seems more likely that domestication-induced body size changes in early livestock species took the form of a reduction in the degree of sexual dimorphism, especially a shortening in the length of the legs of males (Zohary *et al.* 1998, Zeder 2001, 2006b, Helmer *et al.* 2005). Smaller body size in archaeological populations of managed sheep and goats is not seen until sometime after 9,000 cal BP, and it is not clear whether the smaller size of these animals is an artifact of domestication, of climate change, of the introduction of smaller-bodied domestic stock from different regions, or of a general process of body size reduction that began with the end of the last Ice Age and has affected domestic and wild ungulates alike (Zeder 2006b, 2008b).

In addition to these core Near Eastern livestock species, it is likely that other common animal domesticates followed this prey pathway to domestication. This includes East Asian sheep, which genetic data suggest were independently brought under domestication (Guo *et al.* 2005) and perhaps the pigs independently domesticated in East Asia and in Europe (Larson *et al.* 2005, 2007). It is hard to say in the case of pigs, however, whether these separate domestication events followed a commensal path, a prey path, or in the case of the European wild boar the final directed pathway discussed below. Other likely prey pathway domesticates are the humped zebu cattle (*Bos indicus*) and the water buffalo (*Bubalus bubalis*) domesticated in South Asia (Fuller 2006, Kumar *et al.* 2007). The yak (*Bos grunniens*) is another early domesticate that may have been brought under domestication in this way in the Himalayas (Olsen 1990, Guo *et al.* 2006). The mithan (*Bos frontalis*) of South Asia and the Bali cattle (*Bos javanicus*) of island Indonesia, whose origins are poorly understood (Clutton-Brock 1981:137–8), may represent additional examples of prey pathway domesticates. The increasingly well-resolved record of the domestication of South American camelids clearly points to a prey pathway along which the heavy predation of the guanaco (*Lama guanaco*) and the vicuña (*Vicugna vicugna*) developed into initial management and then full domestication of the llama (*Lama glama*) and the alpaca (*Lama pacos*) (see Mengoni-Góñalons and Yacobaccio 2006, Wheeler *et al.* 2006).

Reindeer (*Rangifer tarandus*) may be the most recent, and perhaps last, species to follow a prey pathway to domestication. In many ways, reindeer herding serves as a good model for the initial stages of domestication of other prey pathway domesticates like sheep and goats. The only successfully domesticated cervid species, these cold-adapted gregarious herd animals have been heavily preyed upon by humans since the last Ice Age (Speiss 1989). The close association between hunters and reindeer in the northern Eurasian Holarctic stretches back thousands of years with the loose domestic partnership between humans and reindeer thought to have developed sometime in the past 2,000 to 3,000 years (Mirov 1945, Gordon 2003). Baskin (1974) sees reindeer herding as the product of sophisticated hunting methods in which reindeer hunters, familiar with the migratory routes of wild reindeer herds, drove reindeer into stone traps or human settlements where they could be harvested at will. Over time northern peoples

developed a number of different reindeer herding strategies including a “close” herding system that involves following large demographically diverse herds of migrating animals, a “free-camp” system in which smaller herds are kept within the vicinity of human settlements, and a “loose system” in which free-ranging animals are periodically gathered and moved to different pastures (Baskin 2000). Managed reindeer are exploited for their meat, hides, and antlers, for their use as draft animals and for riding and traction, and, to a lesser extent, for milk. Reindeer herding takes place alongside active hunting of wild reindeer, with domestic females sometimes used in the past as “bait” to attract wild males (Manker 1963:16). As appears to have been the case with other prey domesticates like sheep and goats during initial stages of their management, there are no major morphological differences between wild and domesticated reindeer that would be detectable archaeologically (Clutton-Brock 1981:134).

Recent genetic analysis of modern wild and domestic reindeer from localities across Eurasia (Røed *et al.* 2008) extends the homology between reindeer herding and the initial stages of caprine domestication even further. As with sheep and goat, there is evidence for multiple independent reindeer domestication events within the natural habitat of the wild reindeer. One such “event” was apparently localized in the western part of their range in Fennoscandia, with perhaps two additional events occurring in western and eastern Russia. The high level of genetic diversity in domestic reindeer herds is seen as an artifact of the frequent augmentation of domestic herds with local wild reindeer. The authors of this study also found evidence for the frequent introgression of domestic haplotypes into wild herds. Some wild populations in Finland and Norway and a population in southeastern Russia, however, seem to have contributed no genetic material to domestic stock. Røed *et al.* interpret the different contribution of various wild populations to domestic populations as evidence of the differential domestication potential of wild reindeer. The more gregarious populations residing in open tundra habitats, they argue, were more attractive candidates for domestication. Forest-dwelling populations that may have been less well pre-adapted to domestication, however, seem not to have played a role in this process. This system has many parallels with that documented in the Naderi *et al.* (2008) study of goats in the Zagros, providing a living model of a management system which, though it leaves no mark in the morphology of the managed animals, has a lasting genetic imprint on both managed animals and the wild populations from which they were drawn.

3.3 Directed pathway

The prey pathway was likely driven by the goal of securing a predictable source of protein in the form of animal flesh. But it did not take long before people started to exploit other, largely regenerative secondary animal resources. Recent analysis of lipid residues found in pottery from sites in Turkey and the Levant indicates that dairying may have been well established, especially in northwestern Anatolia,

by about 8,500 calendar years ago (Evershed *et al.* 2008). A figurine of a woolly sheep from the site of Sarab in the highlands of western Iran has been interpreted as evidence that changes in coat composition needed for wool production were in place by about 7,500 calendar years ago (Bökönyi 1977). Finding direct evidence for the use of animals like cattle for traction is difficult, but the discovery of a ceramic bull with a churn on its back in the southern Levant suggests that the use of cattle for both dairy products and labor had been established by 6,000 years ago (Ussishkin 1980). The precedent set by the domestication of former prey species and the broadening of the range of resources extracted from them paved the way for the final category of animal domestication – the directed pathway. This fast-track to domestication begins when humans use knowledge gained from the management of already domesticated animals to domesticate a wild species that possesses a resource or a set of resources that humans see as desirable.

This is likely the pathway followed in the domestication of the horse (*Equus caballus*), which both archaeological and genetic evidence suggests was domesticated, perhaps multiple times, across the steppe regions of central Eurasia (Levine 1999, Olsen 2006, Vilà *et al.* 2006). Possibly originally domesticated to help in the hunting of wild horses (Olsen 2006), domestic horses also provided people with a wide array of primary and secondary resources, including meat, hides, milk, draft, traction, and transport. It is interesting to note that none of the traditional markers used to track domestication in animals that followed the commensal or prey pathways is useful in documenting horse domestication. There are no apparent morphological markers that can be used to discriminate domestic horses from wild horses (*E. ferus*), nor are demographic profiles much use in distinguishing management strategies from prey strategies. Instead, archaeologists employ multiple lines of circumstantial evidence to monitor this process, including butchery practices, evidence of corrals, the presence of quantities of manure signaling corral cleaning, or the use of manure as building materials, and changes in long-distance transport of lithic resources (Olsen 2006). The most recent, and perhaps most compelling, evidence of horse domestication is provided by the successful retrieval of equine milk lipids in 5,500-year-old pottery from northern Kazakhstan (Outram *et al.* 2009).

Donkeys (*Equus asinus*) are another animal that likely entered into the domestic partnership with humans through this route. Genetic evidence puts the initial domestication of two populations of wild Nubian ass (*E. a. africanus*) in northern and northeastern Africa (Kimura *et al.* 2010), with recent thinking crediting their domestication to pastoral people who about 6,000 years ago began to use these desert-adapted animals to carry heavy loads across arid lands (Rossel *et al.* 2008). As with the horse, however, traditional archaeological markers of animal domestication have been of little utility in tracing the process of donkey domestication. Rossel *et al.* (2008) provide compelling evidence for the use of donkeys as beasts of burden in their analysis of ten complete ass skeletons recovered from an early pharaonic mortuary context at Abydos in Middle Egypt. All of these ritually

slaughtered animals show unambiguous signs of, often quite advanced, spondyloarthropathies, vertebral pathologies consistent with the exertion of considerable pressure on the spine. Appendicular skeletal elements of these animals also display considerable compression-induced pathologies, leading to the unmistakable conclusion that these were fully domesticated animals used to carry heavy loads. Morphometric analysis, however, found that the metapodials of these domestic donkeys (the bone thought most likely to respond to any changes in body size or life habits in these animals), closely resemble the metapodials of wild asses (especially the Nubian wild ass) and, in most respects, are quite distinct from the metapodials of modern domestic donkeys. Even though the ass was likely brought under domestication at least 1,000 years before the burial of these ten sacrificial animals, the only hint of domestication-induced morphological change in the Abydos donkeys is a slight modification in metapodial mid-shaft depth and distal breadth dimensions.

Other likely instances of directed domestication are provided by Old World camels, both the one-humped dromedary (*Camelus dromedarius*) of the Arabian Peninsula and the two-humped Bactrian camel (*C. bactrianus*) of Central Asia. Once again there is little direct evidence for camel domestication. There are no archaeologically detectable morphological differences between the domestic and wild two-humped camels (Peters and von den Driesch 1997). Moreover, although there are no longer any wild one-humped camels to compare with the domestic dromedary, there is little evidence of morphological differences in the skeletons of camels from likely pre- and post-domestication contexts in the Arabian Peninsula (Clutton-Brock 1981:124–6). In the absence of distinctive morphological change, the presence of camel dung and hair at the site of Shahri-Sokhta in far eastern Iran and the recovery of figurines of camels attached to clay carts from archaeological sites in Turkmenistan dated to between 3,000 and 2,500 BC have been interpreted as circumstantial evidence that two-humped camels had been domesticated by the third millennium BC (Masson and Sarianidi 1972, Compagnoni and Tosi 1978, but see Peters and von den Driesch 1997). A case of the domestication of the one-humped camel in the Arabian Peninsula is based on the abundance of camel remains from third millennium sites in Oman and associated mortality patterns indicating a shift from a prime adult harvest strategy to an emphasis on the slaughter of juvenile animals (Hoch 1979, but see Uerpmann and Uerpmann 2002). If indeed both these species were brought under domestication during the third millennium BC, the primary target of these two instances of directed domestication may well have been their utility in carrying people and goods across vast arid regions in both Central Asia and in the Arabian Peninsula and the important role these animals might have played in the active global trade networks that developed during this time (Zeder 2006c, Zeder *et al.* 2006).

Elephants, both Asian and African (*Elephas maximus* and *Loxodonta africana*), also represent animals brought under human control for a directed purpose – either for carrying large loads or for heavy labor (a purpose for which Asian elephants are still used today), or for use in hunting, warfare, or in public

spectacles (as was the case for both African and Asian elephants in antiquity and today with circus performers) (Clutton-Brock 1981). Given the long life span of elephants, their slow maturation rate, the difficulty in getting captive elephants to breed, and the relative ease with which captive young adults can be tamed and trained to perform desired tasks, elephants used for these purposes are generally not bred in captivity (Baker and Manwell 1982). Instead, domestication begins anew with each young animal that is captured and tamed. Another captive animal that has been tamed and used for a directed purpose is the cheetah (*Acinonyx jubatus*) that Ancient Egyptians, Assyrians, Mogul emperors, and Medieval European elites kept as pets and hunting companions (Clutton-Brock 1981). Falcons and other trained birds of prey (e.g., *Falco peregrinus* and *Buteo buteo*) used in hunting are also generally not bred in captivity, another example of a captive animal brought under human control for a specific purpose that did not follow the subsequent pathway to full-fledged domestication.

Recent examples of directed domestication include the various carnivore and rodent species, like mink (*Mustela vison*) and chinchilla (*Chinchilla lanigera*) that have been selectively bred for coat quality over the past 100 – 200 years. Other examples of animals following this pathway to domestication also include even more recent domesticates, like buffalo (*Bison bison*), emu (*Dromaius novaehollandiae*), and ostrich (*Struthio camelus*) bred for their meat and hides. Experiments in domestication are currently underway, with mixed success, with a number of terrestrial mammals including red deer (*Cervus elaphus*), Père David's deer (*Elaphurus davidianus*), fallow deer (*Dama dama*), blackbuck (*Antilope cervicapra*), eland (*Taurotragus oryx*), musk ox (*Ovibos moschatus*), and Barbary sheep (*Ammotragus lervia*) (Clutton-Brock 1981:177–87, Hemmer 1990:161–77). The number of freshwater and marine species (both vertebrates and invertebrates) brought under human management has increased markedly over the past 100 years. Ninety-seven percent of the 430 currently managed aquatic species were brought under human control during the twentieth century, 100 of these species in just the past 10 years (Duarte *et al.* 2007). The staggering explosion of aquaculture as a major world-wide industry has momentous implications for the human food supply, for biodiversity, and for the environment.

3.4 A domestication road atlas

There are, then, multiple pathways to animal domestication, which vary in length, direction, and travel time (Figure 9.7). The progress of individual animal domesticates and their human partners down these different paths is highly variable and shaped by the combination of constraints and opportunities, biological and cultural, that these fellow travelers face while they make the domestication journey.

It probably took a long time for animals traveling the commensal pathway to move from being simply habituated to humans and human habitats to developing an active partnership with humans (Figure 9.7a). The timing and the nature of the

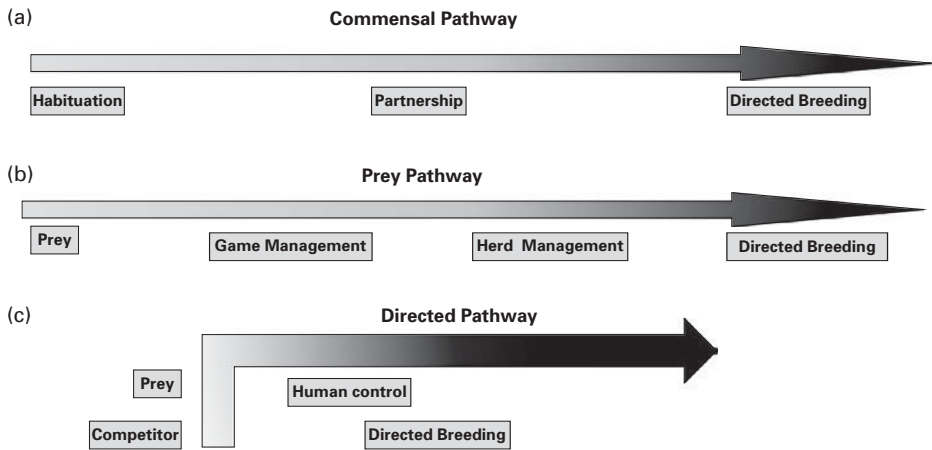


Figure 9.7. Pathways to domestication. (a) Commensal pathway, (b) prey pathway, (c) directed pathway.

forces that propelled the next and final stage of the journey – human-directed breeding and more or less complete subjugation to human control – likely varied in different commensal domesticates. And some animals entering into domestic partnership through this route – like the cat – have arguably never reached this final destination.

While animals traveling the commensal pathway began the journey on their own initiative, animals entering into a domestic partnership with humans through the prey pathway were likely less willing fellow travelers. As with the commensal route, however, progress down the prey pathway was also likely quite slow and possibly circuitous, as generalized hunting strategies evolved into game management strategies aimed at promoting availability of prey species, which, in turn, morphed into the selective harvest of managed animals, followed, at some perhaps quite distant part of the road, by directed breeding (Figure 9.7b). But not all animals traveled this route in the same way, nor did all animals embarking on this pathway reach its conclusion. A strong case can now be made that sheep, goats, and cattle all traveled a quite direct, if lengthy and slow, prey pathway to domestication in central and eastern portions of the Fertile Crescent arc that stretches from southern Iran, across northwestern eastern Iraq and southeastern Turkey, into Lebanon, Israel, and eastern Jordan. Pigs in the central Fertile Crescent, in contrast, may have wandered between prey and commensal pathways at different points of the journey. Moreover while humans and these four future livestock species were beginning down pathways to domestication, in the western arm of this Fertile Crescent region people and gazelle (*Gazella subgutturosa* and *G. gazella*), the primary prey species in the northern and southern Levant, may also have been taking the first tentative steps down a prey pathway to domestication. Gazelle hunting strategies seem to intensify in the Levant at about 12,000 calendar years ago (Munro 2004) and there is some

indication that humans were altering prey strategies to promote availability of this key resource in ways that were having some impact on the demographic structure of gazelle populations (Davis 1983, Henry 1989, Cope 1991, but see Sapir-Hen *et al.* 2009). Parallels can be found between the corrals and traps used much later by Eurasian Arctic peoples early on in the process of reindeer domestication (Baskin 1974) and the stone kites and possible corrals found throughout the Levant that are thought to have been used to capture migrating gazelle (Legge and Rowley-Conwy 1987, Betts and Yagodin 2000, Bar-Oz *et al.* 2011). Redding (2005) has recently suggested these structures may also have served as holding areas for animals that could be consumed as needed, clearly a step toward animal management. Gazelle, however, are behaviorally less well suited than sheep and goat to domestication. They have very strongly developed flight reflexes and an aversion to penning, and are highly territorial and unlikely to breed well in captivity (Clutton-Brock 1981:172). These behaviors are thought to have made it impossible for gazelle to travel much further down the prey pathway than the early stages of game management.

The final directed pathway is a much shorter and speedier route to animal domestication. Animals traveling down this path may have begun as human prey or competitors for prey, or may have had little or nothing to do with humans. However, once embarked on this pathway they took an immediate and abrupt departure from a free-living state to one in which they were under tight human control that often involved intensive and deliberate breeding to enhance targeted resources. Animals selected for the directed pathway may have possessed few of the pre-adaptive behaviors that qualified other animal domesticates for a trip down either the commensal or prey pathways, and their domestication likely required intensive efforts to overcome behavioral and biological barriers to domestication. Today this route has become a kind of domestication super-highway as animals that previously would never have been considered candidates for domestication are brought under human control through the application of increasingly sophisticated technology for animal breeding and care, and the enhanced understanding of animal behavior, reproduction, and biological requirements coming out of the animal sciences (Price 2002:22).

4 Questions for future research

Categorization of the various pathways to animal domestication in this way raises a number of questions that point to productive areas for future research. First, it would be interesting to know whether there are differences in the timing and the nature of the behavioral, physiological, and morphological responses animals make to the selective pressures they experience along these different pathways to domestication. A related question asks whether these selective pressures leave distinctive genetic, morphological, or other archaeological markers that can be used to detect the various paths taken to domestication. Are animals that enter

domestication through a commensal route, with its long “getting-to-know-you” phase of habituation to humans and human environments, tamer and more integrated into human society than animals that traveled the prey pathway? Are the changes in cranial form seen as an early marker of domestication in dogs and pigs, but not as apparent in animals such as sheep, goats, or horses, an artifact of a more prolonged and perhaps more intense selection for human habitation? If so, why is it that other animals that may have taken this same commensal route, such as the cat, do not display similar cranial morphology? Why is there often little evidence of morphological change in animals brought into the domestic relationship by way of the directed route? Are there different genetic signatures that can be used to trace the behavioral adaptations that grew out of the commensal relationship and differentiate them from those that arose through the prey pathway? Does the intensive, focused selection for specific traits under directed domestication leave a distinctive genetic signature distinguishable from the genetic signatures left by the broader play of selective factors and random events that shaped both the commensal and prey routes?

The different capacities for feralization of different domesticates and the residual imprint of domestication seen on these animals raises another set of questions. Among them, are commensal domesticates more successful feral animals because they can revert to the commensal behaviors that brought them into the relationship in the first place? How do feral commensal domesticates vary in behavior, physiology, and morphology from commensal species that never traveled any further down this path?

Looking forward, this discussion raises a series of questions about ongoing processes of domestication and breed improvement. Are there lessons that might be drawn from the different pathways humans and animals followed to domestication in ancient times that might be applied to current-day breed improvement programs? Do ancient efforts at game management and initial herd management have bearing on current-day ranching practices directed at animals like the eland and the fallow deer? Can this perspective help animal scientists better balance the dual goals of enhancing both animal productivity and animal welfare (Grandin and Dessing 1998, Price 2002:204–29, Keeling and Jensen 2002)? What are the environmental and biodiversity impacts of the massive wave of recent directed domestications, especially those involving aquatic species, and how can a broader understanding of the multiple pathways to domestication help mitigate these impacts?

Finally, recognition of the multiple pathways to domestication and their impact on domestic animals has a bearing on a range of issues involving the care and welfare of captive animals, as well as conservation efforts directed at endangered species (O'Regan and Kitchener 2005). Can these different models of domestication contribute to a better understanding of the impact of captivity on wild animals kept in zoos or in captive breeding programs? Are there parallels to be drawn between feralized domesticates and the reintroduction of captive animals into the wild?

Answering these questions requires drawing broadly from genetics, animal sciences, and archaeology. As this review has shown, researchers based in each of these general disciplinary areas are actively contributing to a large and growing body of knowledge on animal domestication and the potential for cross-illumination between these different perspectives is only just beginning to be realized. Clearly the interdisciplinary model set by Jack Harlan in his career-long study of crop evolution holds much promise for the study of animal domestication. And it is rewarding to see researchers from all of these different disciplinary backgrounds included in the second Harlan International Symposium and the publication of the proceedings of that stimulating meeting. Hopefully, contributors to the third Harlan International Symposium will be able to report considerable progress in addressing the questions raised here and other questions about pathways to animal domestication.

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10 Genetics of Animal Domestication

Leif Andersson

Domestic animals show an amazing phenotypic diversity in form, color, behavior, and as regards their adaptation to various environments and production systems (Figure 10.1). Domestication took place 5,000 to 10,000 years ago for the major species of domestic animals and probably even earlier than that for the dog. It is now an exciting time for studying the evolutionary history of animal domestication thanks to the development of powerful tools for genetic analysis. We are now in a position where we can identify major genetic changes associated with domestication. This research is not only of interest for its own sake but it is also of general interest as a model for evolutionary biology and it will lead to new knowledge concerning gene function and genotype–phenotype relationships of interest for human medicine. Considerable progress has been made in the past 10 years as regards when and where animal domestications took place (Giuffra *et al.* 2000, Vilà *et al.* 2001, Savolainen *et al.* 2002, Bruford *et al.* 2003, Larson *et al.* 2005). However, the aim of this paper is to discuss how the genetic basis for phenotypic evolution in domestic animals can be revealed and how far we have come in this process and to give two examples where the alleles underlying phenotypic traits not present in the wild ancestor have been identified.

1 Most genetic diversity pre-dates domestication

A common misconception about domestic animals is that they are highly inbred. That is true if one considers certain breeds; in particular, the dog is subdivided into many small populations that are more or less inbred. However, across populations of domestic animals there is an extensive amount of genetic diversity at the DNA level. For instance, a pair of chicken chromosomes shows on average 5 sequence differences per 1,000 base pairs (International Chicken Polymorphism Map Consortium 2004). The corresponding figure for humans is only 1 difference per 1,000 base pairs. Other species of domestic animals show nucleotide sequence diversities



Figure 10.1. Phenotypic diversity of domestic chicken in comparison with the phenotype of their wild ancestor, the red junglefowl. Water color painting by Staffan Ullström.

in the same range as humans do. The reason for the high or fairly high degree of sequence diversities among domestic animals is that most if not all domestication events involved species with large populations with high or fairly high levels of genetic diversity. It is still controversial whether domestication involved a population bottleneck that significantly reduced genetic diversity or whether domestication took place over a longer period of time and at multiple sites so that a considerable amount of genetic diversity was maintained in the domesticated form. The former scenario has been suggested for cattle (Bruford *et al.* 2003). In contrast, data from the pig and the chicken have been interpreted to indicate that domestication did not involve a severe population bottleneck since the domestic

forms show an amount of genetic diversity similar to that present in their wild ancestors (International Chicken Polymorphism Map Consortium 2004, Fang and Andersson 2006). Fang and Andersson (2006) found clear evidence for signs of previous population bottlenecks in both European and Asian pigs but the results indicated that the bottleneck took place prior to domestication, possibly a consequence of the effects of the most recent glaciation period.

It is easy to demonstrate that the origin of most of the sequence diversity we observe in contemporary populations of domestic animals pre-dates domestication. The expected number of nucleotide differences between a pair of DNA sequences is a function of their coalescence time, i.e., the time since they diverged from a common ancestral sequence. The accumulation of sequence differences is slow, owing to the very high accuracy of DNA replication. Let us consider the human and the chimpanzee: they diverged from a common ancestor about 5 million years before present and the average sequence difference across the genome is c.1.2%. Thus, it takes millions of years to accumulate a 1% sequence difference and it takes hundreds of thousands of years to accumulate a 0.1% sequence difference. Even though the generation time is significantly shorter in the chicken we can safely conclude that most of the sequence diversity we observe in this species pre-dates domestication, as the average frequency of nucleotide differences is about 0.5%. The same argument holds up for other domestic animals, which show average nucleotide differences around 0.1%. This also implies that the time since domestication (<10,000 years) is too recent for the domestic animals to show a notable sequence divergence from their wild ancestors. Thus, when analyzing selectively neutral loci domestic animals appear like subpopulations of their wild ancestors and it is not easy to distinguish a domestic animal from its wild ancestral form unless one focuses on those loci that have responded to selection during domestication and selective breeding. At such loci it is possible to find sequence variants that are common among domestic animals but rare or completely absent in the wild ancestor. At other loci, the domestic animal and wild ancestor often share the same sequence polymorphism profile.

2 Selection on new mutations or standing genetic variation?

Since most of the genetic diversity that we can observe in domestic animals pre-dates domestication, it is relevant to ask whether the dramatic changes in phenotype that have occurred represent selection acting on new mutations or the standing genetic variation that existed prior to domestication. We have good reasons to assume that both sources of variation have contributed. A general rule is that mutations with large effects in most cases represent new mutations. First, the effects of such mutations are easy to observe and can therefore be fixed by phenotypic selection. Second, mutations with large effects are more likely to be harmful under natural conditions and therefore eliminated by purifying selection. Human-driven phenotypic selection during the early history of animal

domestication is more likely to have involved alleles with large effects, whereas animal breeding methods have become more and more precise during the past hundred years, so that allelic variants with tiny effects could be selected. In the latter case it is very likely that a good proportion of the selection response reflects selection on standing genetic variation. Furthermore, it is important to recognize that artificial and natural selection for fitness are always ongoing in parallel in domestic animals. Domestication can be seen as a genetic adaptation to a new environment, the farm. This is partly a result of the way humans select breeding animals, but natural selection also contributes. Natural selection involves, for instance, resistance to infectious diseases, reproductive traits, and stress tolerance. Humans can only select breeding animals from among those that survive to reproductive age and are able to reproduce in the farm environment. This natural selection may well involve alleles with tiny effects that existed prior to domestication.

The melanocortin 1 receptor locus (*MC1R*) provides an illustrative example where selection for new mutations predominates. *MC1R* has an important role in melanocyte biology as *MC1R* signaling determines the switch between production of black eumelanin and red pheomelanin. In brief, *MC1R* signaling leads to production of black pigment whereas lack of *MC1R* signaling leads to the production of red pigment. Most wild species exhibit a camouflage-colored coat that is composed of a mix of red and black pigment (Figure 10.2a). Fang *et al.* (2009) resequenced the single *MC1R* exon from domestic pigs representing 50 breeds from Europe and China as well as European and Asian wild boars. Pigs were independently domesticated from European and Asian wild boars (Giuffra *et al.* 2000, Larson *et al.* 2005) and it has been estimated that these two subspecies diverged from a common ancestor >500,000 years before present (Kijas and Andersson 2001). We found a total of eight nucleotide substitutions among wild boar *MC1R* sequences and all were synonymous, i.e., they did not change the *MC1R* protein sequence (Fang *et al.* 2009). This shows that camouflage color in wild boars is maintained by purifying selection. In sharp contrast, eight out of nine substitutions found among domestic pigs changed the protein sequence. Several alleles differed by up to three substitutions from the wild-type sequence. This is illustrated by the *Ep* allele for black spotting, which involves two functionally important mutations (Figure 10.2b). It contains a mis-sense mutation associated with black color and a frameshift mutation (insertion of two C nucleotides at nucleotide 67) that is expected to lead to red color due to the lack of a functional *MC1R* receptor (Kijas *et al.* 2001). However, the black spots occur because the frameshift mutation is somatically unstable and may be lost; when this happens the reading frame is restored and the black spots occur!

The highly significant excess of mutations that change the *MC1R* protein sequence shows that humans have cherry-picked novel mutations to intentionally alter the coat color of pigs. Those mutations would be eliminated in the wild due to purifying selection. So, why have humans actively changed the coat color of domestic animals? One reason could be that it has facilitated animal husbandry

(a)



(b)



Figure 10.2. (a) Camouflage coat color in wild boar piglets carrying the wild-type allele at the *MC1R* locus (Photo by Anneli Andersson, Linköping University). (b) Black-spotted piglets from the Swedish Linderöd breed. The black spots are caused by the combined effect of two consecutive mutations in the *MC1R* gene. Photo: Paul Seugling.

as it is easier to keep track of an animal with a conspicuous color than a camouflage-colored one. Another reason could be that altered color has been preferred because it was used to distinguish the improved domestic forms from their close wild relatives. Finally, human preference for novelties could also have contributed.

3 Genetic dissection of phenotypic traits

Different approaches can be employed to reveal genetic changes associated with domestication. The chances of obtaining conclusive evidence that a certain mutation is associated with domestication are of course better when a direct comparison can be made with an existing wild ancestor such as the wolf, the wild boar, or the red junglefowl than in those species where the wild ancestor is extinct as is the case for the ancestor of domestic cattle, the aurochs. However, it may be possible to utilize ancient DNA from aurochs to test for the presence of specific mutations (Svensson *et al.* 2007). One possible approach is to investigate candidate genes that are presumed to be important for a certain trait. This can be very successful and quickly lead to important results. However, for most traits this is a very uncertain approach that often leads to inconclusive results. The reason is that most traits have many potential candidate genes and the causative mutation may be regulatory in nature and located hundreds of kilobases away from the affected coding sequence. However, one possibility is to search for footprints of selection such as the selective sweeps that occur when a favorable mutation becomes fixed in a population (Andersson and Georges 2004).

A more powerful approach is to perform cross-breeding experiments using the wild ancestor where possible. We have generated such intercrosses for both pigs and chickens with the aim of studying the genetics of domestication. Already in the late 1980s we developed an intercross between the European wild boar and Large White domestic pigs comprising 200 F₂ progeny (Andersson *et al.* 1994). Here are some highlights from the characterization of this material.

We showed that the difference in coat color between wild boars and Large White pigs are primarily controlled by two loci, the *MC1R* locus discussed above and the *KIT* locus associated with Dominant white color. *KIT* receptor signaling plays a crucial role during the migration of neural-crest-derived cells during embryogenesis, and pigmentation variants caused by allelic variation in the *KIT* gene are due to missing melanocytes in skin and hair follicles. The *Dominant white* allele in pigs is another example of an allele that results from two consecutive mutations, a 450 kb duplication encompassing the entire coding sequence (Giuffra *et al.* 2002) and a splice mutation leading to skipping of exon 17 (Marklund *et al.* 1998). The duplication must lead to dysregulated expression of *KIT* during melanoblast migration in the embryo because the *Patch* allele that includes the duplication but not the splice mutation is associated with partial loss of pigmentation (Johansson *et al.* 1992). The splice mutation occurs in one of the

two *KIT* copies and results in a *KIT* receptor with normal ligand binding but defective tyrosine kinase signaling. This leads to a drastic reduction of *KIT* signaling and, in combination with the presence of the duplication, essentially a complete loss of hair and skin pigmentation. Thus these pigs are white because they do not have any pigment cells in skin and hair. A *KIT* allele containing the splice mutation but not the duplication would be lethal in the homozygous condition because *KIT* signaling is essential also for the development of hematopoietic cells. Thus, the *Dominant white* allele in pigs is unique in having an extremely strong effect on pigmentation but only mild negative effects on hematopoiesis (Johansson *et al.* 2005).

An interesting aspect of the *Dominant white* allele is that the presence of the large duplication makes it genetically unstable so that unequal crossing over can either lead to a haplotype with one copy or three copies (Pielberg *et al.* 2002). Thus, *KIT* haplotypes with one, two, or three copies segregate in commercial populations of white pigs (e.g., Landrace and Large White) which explains why there is still variation in coat color in these populations despite the fact that breeders have been trying to fix the white color for the past hundred years. This means that white pigs carrying the *KIT* duplication that become feral will sooner rather than later return to wild type because haplotypes with a single *KIT* copy and without the splice mutation will be generated by unequal crossing-over. The reverted allele will have a strong selective advantage because it provides camouflage and protection from sunlight.

There has been very strong selection for lean growth (high muscle growth and reduced fat deposition) in domestic pigs in the past 50 years owing to the consumer demand for meat with a low fat content. In contrast, in the past when most humans had physically demanding work in agriculture or industry, the selection criterion was pigs with a high fat content because of the demand for food with high energy content. An obvious phenotypic difference between modern pigs and wild boar is therefore that the latter grow slower and store much more fat when feed resources are plentiful, which is an obvious adaptation for surviving periods with poor feed resources. In our intercross between the European wild boar and Large White pigs, we identified two quantitative trait loci (QTLs) with large effects on fat deposition. These two loci must have contributed significantly to the reduction of fat deposition and increase in muscle content in modern pigs. One locus was mapped to chromosome 4 and affects both visceral and subcutaneous fat but the causative gene(s) for this QTL has (have) not yet been identified (Andersson *et al.* 1994, Berg *et al.* 2006). The second locus was assigned to the distal tip of pig chromosome 2 and the allele from the domestic pig increased muscle growth by 3%–4%, reduced backfat thickness, and increased the size of the heart (Jeon *et al.* 1999). The gene encoding insulin-like growth factor 2 (*IGF2*) was identified as the prime positional candidate gene underlying this QTL. Family segregation analysis was used to put together a panel of paternal chromosomes carrying either the wild-type allele (*q*) or the mutant allele (*Q*) increasing muscle growth. We resequenced about 28 kb from *IGF2* and its flanking region and

obtained conclusive genetic evidence showing that a single base-pair substitution in intron 3 must be the causative mutation (Van Laere *et al.* 2003). The mutation is located in a CpG island and 16 base pairs around the mutated site showed 100% sequence identity among eight mammalian species, including humans. Experimental work showed that the mutation disrupts the interaction with an unknown nuclear factor and that it is a *cis*-acting regulatory mutation that markedly upregulates IGF2 in muscle tissue after birth (Van Laere *et al.* 2003). This mutation has a huge impact on pig production efficiency and has gone through a selective sweep in many of the most widely used commercial pig populations in the Western world. Most of these populations are fixed or close to fixation for this favorable mutation.

We have also generated an intercross between the red junglefowl and White Leghorn chickens. The intercross comprises as many as 800 F₂ birds to give good statistical power in the genetic analyses. Data on a large number of phenotypic traits have been collected including plumage color, body mass and growth, egg production, bone density, body composition, and behavioral traits. A genome scan with more than 500 genetic markers has been completed. Here are some highlights from the analysis of these data. We have identified some of the major loci explaining differences in plumage and skin color between the red junglefowl and strains of domestic chicken: Dominant black color was shown to be caused by a mutation in the *MC1R* gene (Kerje *et al.* 2003b), the same gene that also affects coat color in horses, pig, cattle, sheep, and dogs; Dominant white color is caused by a mutation in the *PMEL17* gene (Kerje *et al.* 2004); the sex-linked Silver plumage color that lacks expression of red pheomelanin is due to a mutation in *SLC45A2* (Gunnarsson *et al.* 2007); and finally the yellow skin phenotype is controlled by the *BCDO2* locus (see below).

Striking differences between the red junglefowl and the White Leghorn chicken include a two-fold difference in adult body mass, changes in various morphological traits, marked changes in behavior, and enormous differences in the number of eggs produced since the White Leghorn chickens have been strongly selected for egg production. A consequence of the strong selection for egg production is that females in such lines (layers) have high fat deposition and high bone density when egg production starts, which allow them to mobilize fat and calcium for production of egg yolk and eggshells. We have been able to identify QTLs for all of these different types of traits (Carlborg *et al.* 2003, Kerje *et al.* 2003a, Keeling *et al.* 2004, Schütz *et al.* 2004, Wright *et al.* 2006, Rubin *et al.* 2007, Wright *et al.* 2008). We were able to identify some QTLs with very large effects on growth (Kerje *et al.* 2003a). Two QTLs explained as much as 50% of the difference in body mass between the White Leghorn and red junglefowl populations. Interestingly, one of these loci was colocalized with QTLs affecting body composition, egg size, and some behavioral traits (Schütz *et al.* 2004). The genes underlying these QTLs have not yet been identified and therefore we do not know whether they represent a few loci with pleiotropic effects on several traits or clusters of QTLs each affecting different traits. This is still work in progress. The fact that these loci have strong effects on

some of the key features of the domestic chicken such as growth patterns, behavior, and egg production and that we detected them as genetic differences compared with the red junglefowl suggest that they may very well represent some of the key changes that occurred during chicken domestication.

4 Yellow skin in chickens

A large proportion of domestic chickens around the world show the yellow skin phenotype (Figure 10.3). Yellow skin was one of the traits Bateson (1902) included



Figure 10.3. Young Icelandic hen with bright yellow legs due to homozygosity at the *yellow skin* gene allowing deposition of yellow carotenoids in skin. Photo: Atli Arnarson.

in the first demonstration of Mendelian inheritance in animals. *Yellow skin* was found to be recessive to the *White skin* allele that is present in the red junglefowl. The yellow color does not represent a pigment the bird makes itself, but carotenoids that the bird obtains from its diet. The more carotenoids in the feed, the brighter the skin color. Carotenoid pigmentation is extremely important among birds and other animals: examples include the bright yellow bill of the blackbird and the pink color of the flamingo. Carotenoid-based ornaments (skin or feathers) in wild birds are considered to be an honest signal of an individual's nutritional status or health, reflecting its foraging efficiency or immune status, and are therefore implied to affect sexual attractiveness (Blount *et al.* 2003).

We identified the gene for yellow skin color by linkage mapping within families combined with Identical-by-Descent analysis across breeds with this phenotype (Eriksson *et al.* 2008). The phenotype is caused by one or more *cis*-acting regulatory mutations affecting the expression of *BCDO2* encoding a beta-carotene dioxygenase 2 enzyme that cleaves colorful carotenoids into colorless apocarotenoids. We showed that the wild-type and mutant alleles are expressed at the same level in the liver but only the wild-type allele is expressed in the skin. This suggests a mechanism where carotenoids are taken up in skin in both yellow-skinned and white-skinned animals, but in the latter carotenoids are degraded by the action of the *BCDO2* enzyme.

We searched for the causative mutation by resequencing 24 kilobases of genomic DNA encompassing most of the *BCDO2* gene, showing complete association with the yellow-skin allele among European chicken populations (Eriksson *et al.* 2008). To our surprise, we found that *yellow skin* and *white skin* haplotypes showed an 0.8% sequence difference in this region and no intermediate forms were found. This suggested that the two forms have evolved independently over a considerable amount of time. We therefore sequenced the same region from closely related species, namely the gray junglefowl, the green junglefowl, and the Ceylon junglefowl. The sequence results revealed a very clear pattern. The *yellow skin* sequence clustered with sequences from the grey junglefowl and the Ceylon junglefowl, whereas the *white skin* sequences clustered with sequences from the red junglefowl. Therefore, the *yellow skin* haplotype must have been introgressed into the domestic chicken from a closely related species of junglefowl, most likely the gray junglefowl. This provided the first conclusive evidence that the domestic chicken has a polyphyletic origin although most of its germplasm, probably 95% or more, originates from the red junglefowl. Our study settled the long-standing question of whether the domestic chicken has a monophyletic origin (one ancestral species) or a polyphyletic origin (more than one ancestral species), a debate that had been ongoing for centuries (Darwin 1868, Hutt 1949).

So why have humans to a large extent replaced the *wild-type* (*white skin*) allele with the *yellow skin* allele in domestic chicken? This must have happened early during domestication since the trait is so widespread (Eriksson *et al.* 2008). At that time chickens were not fed to any large extent and they foraged for food around the settlement, a form of chicken production still in place in many developing

countries. It is thus possible that early farmers noted that chickens with bright yellow skin had better survival and/or better egg production since previous studies have indicated that access to carotenoids is a limiting factor for egg-laying capacity (Blount 2004). This does not imply that birds homozygous for the *yellow skin* allele are better foragers than white-skinned birds, but the yellow skin phenotype acts as a sensor of nutritional status. However, we cannot exclude the possibility that the yellow-skinned phenotype was favored simply because it appeared more appealing. In some countries like Mexico, the yellow-skin phenotype is favored to the extent that the feed is supplemented with carotenoids to enhance the yellow color, which illustrates human preference for a traditional appearance of food.

5 Graying with age in horses

Graying with age is one of the most charismatic phenotypes selected during animal domestication (Figure 10.4). White horses are born colored, but the graying process starts during their first year of life and by the age of 6–8 years they are usually entirely white. They lose hair pigmentation but maintain normal skin and



Figure 10.4. Two white Lippizaner mares with their colored foals in front of the Piber castle in Austria. The two foals most likely carry the *Grey* mutation and are therefore expected to show the spectacular white coat color by the age of six to eight years. Photo: Meike Pachner, Stud Piber, and the Spanish Riding School in Vienna.

eye pigmentation and show no hearing loss. However, a large proportion develop a form of melanoma but often late in life. No mutation has had a higher impact on human culture than *Grey*. All over the world the white horse is used as a symbol for prestige, beauty, and dignity. The oldest written record for the presence of white horses that we have been able to find is the Greek historian Herodotus, who claims that the Persian emperor Xerxes (in reign 485–465 BC) kept sacred white horses. The unique status of the white horse is apparent from numerous paintings and myths (Unicorn, Pegasus, “the prince on a white horse”, etc.). Numerous hotels, pubs, and restaurants are named after the white horse. The Harlan II symposium was held at the campus of UC Davis. Walking to and from the symposium venue I was amused to see that the white horse was used in the logo for the local American football college team!

Graying with age is inherited as a dominant mutation with full penetrance. The causative mutation was identified by combining linkage analysis within families with high-resolution Identical-by-Descent mapping (Rosengren Pielberg *et al.* 2008). We analyzed about 700 gray horses representing eight different breeds. They all shared the same causative mutation, a 4.5 kb duplication in intron 6 of the *STX17* gene, as well as a 352 kb haplotype showing complete association with *Grey*. This shows that all gray horses, at least those 700 we have tested, have inherited the *Grey* mutation from a single common ancestor that must have lived more than 2,500 years before present. The mutation has then spread over the world due to the strong preference for this phenotype; about 10% of all contemporary horses carry the mutation.

The causative mutation is once again a *cis*-acting regulatory mutation that leads to an upregulated expression of both *STX17* and the neighboring *NR4A3* gene in melanoma tissue from gray horses (Rosengren Pielberg *et al.* 2008). It is still an open question whether the upregulated expression of one of these genes underlies all aspects of the gray phenotype or whether both genes contribute. This is the subject of ongoing follow-up studies.

6 Emerging opportunities

There has been a very rapid development of new tools and resources for genetic and genomic analysis over the past 20 years. This has led to a rapid increase in knowledge in all areas of biology, as has been illustrated in this chapter as regards the evolutionary history of domestic animals. We are now facing a new revolution in the biological sciences as new cost-effective methods for high-throughput sequencing are emerging. At present there are two major competing technologies available for this purpose: the HiSeq 2000 instrument from Illumina and the SOLiD instrument from Applied Biosystems. Each of these instruments can generate huge amounts of sequence information in a single run (100–300 Gbp) at reasonable cost. It is therefore possible to resequence the entire genome from individuals or pools of individuals representing different breeds of

domestic animal. This approach can be used to identify mutations that occur at high frequency in domestic animals but are rare or absent in their wild ancestor. We can search for regions of the genome with strong signals for selective sweeps like the *IGF2* region in pigs (Van Laere *et al.* 2003) or the *yellow skin* locus in chickens (Eriksson *et al.* 2008). We can investigate to which extent sequence duplications and deletions have contributed to the evolution of domestic animals. During the next ten years this type of information, combined with genetic studies of genotype–phenotype relationships, should take us a long way towards the reconstruction of the evolutionary history of domestic animals. As this knowledge accumulates it will be more and more rewarding to combine genetic and archaeological studies using remnants from early domestic animals as this will allow us to detect when and where certain key genetic changes took place. There is no doubt that this field of research will be very exciting over the next ten years!

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11 Genome-Wide Approaches for the Study of Dog Domestication

Bridgett M. vonHoldt, Melissa M. Gray, and Robert K. Wayne

Dogs display a remarkable amount of phenotypic diversity in coat color, texture, and cranial and skeletal proportions, yet as a species they are distinct from wild canids (Wayne 1986a,b). Similarly, considerable variation in behavior and physiology are evident among breeds and between dogs and wild species (Hart 1995, Hare *et al.* 2002, Spady and Ostrander 2008). Considering the great diversity of dogs, Darwin and others postulated that domestic dogs were founded from more than one canid species (Darwin 1859, Lorenz 1954, Coppinger and Schneider 1995). However, molecular data showed conclusively that dogs originated from the gray wolf (*Canis lupus*) (Morey 1994, Vilà *et al.* 1997, Savolainen *et al.* 2002, Pang *et al.* 2009). Nonetheless, because of the morphologic divergence between dogs and gray wolves, identifying a specific ancestral gray wolf population is difficult.

The earliest proto-dogs were likely similar to wolves but subsequent evolution has rendered all breeds and dog populations as morphologically distinct from wild progenitors (Zeuner 1963, Epstein and Mason 1972, Olsen 1985, Morey 2006). Archaeological evidence suggests that the earliest dogs are from central Russia (15,000 y bP, Sablin and Khlopachev 2002), Western Europe (31,000 y bP, Germonpre *et al.* 2009) or the Middle East (12,000 y Bp, Nobis 1979, Olsen 1985, Davis 1987, Dayan 1994, Clutton-Brock 1995, Morey 2006). A problem with the archaeological data is that putative ancient dogs may in reality be differentiated varieties of local wolves (e.g., Leonard and Wayne 2008) or already so derived that the origin may be elsewhere. By contrast, East Asia is supported as a center of origin for dogs based on higher mitochondrial DNA (mtDNA) sequence diversity in dogs that originated there (Savolainen *et al.* 2002). However, mtDNA sequence is information from essentially a single gene and thus may not represent the history of the genome or the actual species tree (Wayne *et al.* 2006). For example, high mtDNA sequence diversity may reflect a center of regional trade rather than the location of species origin (Wayne *et al.* 2006). Consequently, genome-wide approaches are needed to sample a wider variety of gene histories and to provide a better consensus of evolutionary history.

The dog genome is likely affected by historical admixture with wolves from a variety of geographic regions (e.g., Randi *et al.* 2000, Randi and Lucchini 2002, Anderson *et al.* 2009), and therefore, different parts of a breed genome may share ancestry for different wolf populations. Genome-wide approaches provide a direct evaluation of past admixture and potentially allow a partitioning of genomic histories (e.g., Patterson *et al.* 2006). In this chapter, we discuss some of the new genome-wide approaches that utilize: (1) the canine genotyping array containing 40,000–60,000 single nucleotide polymorphisms (SNPs) and (2) SNPs based on extensive resequencing efforts of six genomic regions, including the insulin growth factor gene (*IGF1*) that plays an important role in size variation in dogs (Sutter *et al.* 2007). We will begin by briefly summarizing previous research and then discuss new genome-wide approaches, their interpretative problems, and some preliminary results.

1 Previous research

Genetic data have consistently supported an origin of dogs from gray wolves although specific progenitor populations were never identified. Dogs are most similar to gray wolves with respect to single-copy DNA and albumins (Seal *et al.* 1970, Sarich 1977, Wayne *et al.* 1989) and they share the greatest proportion of allozyme protein variants (Ferrell *et al.* 1978, Wayne and O'Brien 1987). However, few allozyme alleles are uniquely shared between dogs and gray wolves as these alleles are also found in closely related canids such as golden jackals (*Canis aureus*) and coyotes (*C. latrans*) (Wayne and O'Brien 1987). Gray wolves and dogs have identical chromosome complements (Wayne *et al.* 1987a, b) but their karyotypes are indistinguishable from those of other species in the genus *Canis* (coyotes, wolves, jackals) (Wurster-Hill and Centerwall 1982). More highly variable markers, such as short tandem repeat loci, often called microsatellites, promised greater resolution (Bruford and Wayne 1993). Although more alleles are shared between dogs and wolves than between dogs and other canids, the genetic distances were small and microsatellites did not provide definitive conclusions about the origin of the dog (see Roy *et al.* 1994, García-Moreno *et al.* 1996). As many mitochondrial genes have a higher rate of sequence evolution than nuclear genes, DNA sequencing, especially of the rapidly evolving mitochondrial DNA control region, would potentially provide a more definitive approach for reconstructing the history of domestication. The first studies focusing on mtDNA variation clearly suggested a close ancestry of gray wolves and dogs. However, these studies involved indirect sequencing techniques and a limited sample of both species (Wayne *et al.* 1992, Gottelli *et al.* 1994). Subsequently, this result was confirmed with direct sequencing of the mtDNA control region (Okumura *et al.* 1996, Tsuda *et al.* 1997, Vilà *et al.* 1997).

The first large-scale study directed at understanding dog origins and the timing of domestication utilized a geographically broad sampling of domestic dogs and

gray wolves and several other wild canid species (Vilà *et al.* 1997). This study included 162 wolves from 27 populations from throughout Europe, Asia, and North America and 140 dogs representing 67 breeds. The mean sequence diversity within dogs was $5.30\% \pm 0.17$, a value surprisingly large and very similar to the value of $5.31\% \pm 0.11$ found in gray wolves. This result suggested that dogs were not founded by a small number of gray wolves or, if they were, repeated interbreeding with wolves maintained high levels of variation (Tsuda *et al.* 1997). The importance of backcrossing has recently been confirmed by study of genes from the major histocompatibility complex (MHC) that showed high levels of variation in dogs (Vilà *et al.* 2005). Because the sequence substitution rate of the MHC is low, this diversity likely originated in wolves and was transferred to dogs through hybridization (e.g., Randi *et al.* 2000, Randi and Lucchini 2002, Anderson *et al.* 2009).

To determine the evolutionary relationships of mitochondrial sequences in dogs and gray wolves, phylogenetic trees were constructed (Figure 11.1). Four sequence groupings or clades were suggested by the topology of the sequence tree (Figure 11.1; I–IV as in Vilà *et al.* 1997). These clades and several other dog–wolf clades have been independently discovered by other researchers (Okumura *et al.* 1996, Savolainen *et al.* 2002, Verginelli *et al.* 2005, Li *et al.* 2008) and suggest that either wolves were domesticated in several places and/or at different times or that there was one domestication event followed by several episodes of admixture between dogs and wolves. For example, in clade IV, a wolf sequence is identical to a dog sequence, suggesting a more recent interbreeding or origination event. The geographic origins of dogs have been difficult to resolve because, unlike for domestic cats (Driscoll *et al.* 2007), the wolf progenitor of dogs had high dispersal abilities and consequently, mtDNA haplotypes are shared widely among wolf populations (Vilà *et al.* 1999). However, in a recent study, Savolainen *et al.* (2002) found that the mitochondrial DNA diversity present in East Asian dogs is much larger than in other areas, implying East Asia as the place of origin. Additionally, by dividing clade I into multiple sequence groups and estimating their common ancestry, the authors concluded that an origination date approximately 15,000 to 40,000 years ago was conceivable. This range of dates is consistent with the archeological record (see above), although it does not agree with a date of >100,000 years before present as suggested by the earlier mitochondrial DNA sequence study (Vilà *et al.* 1997).

2

Molecules versus morphology

The archaeological record suggests that the first domestic dogs were found in the Middle East or Central Europe about 14,000 to 31,000 years ago (Nobis 1979, Olsen 1985, Dayan 1994, Clutton-Brock 1995, Sablin and Khlopachev 2002, Germonpre *et al.* 2009). Most early dogs are morphologically distinct from gray

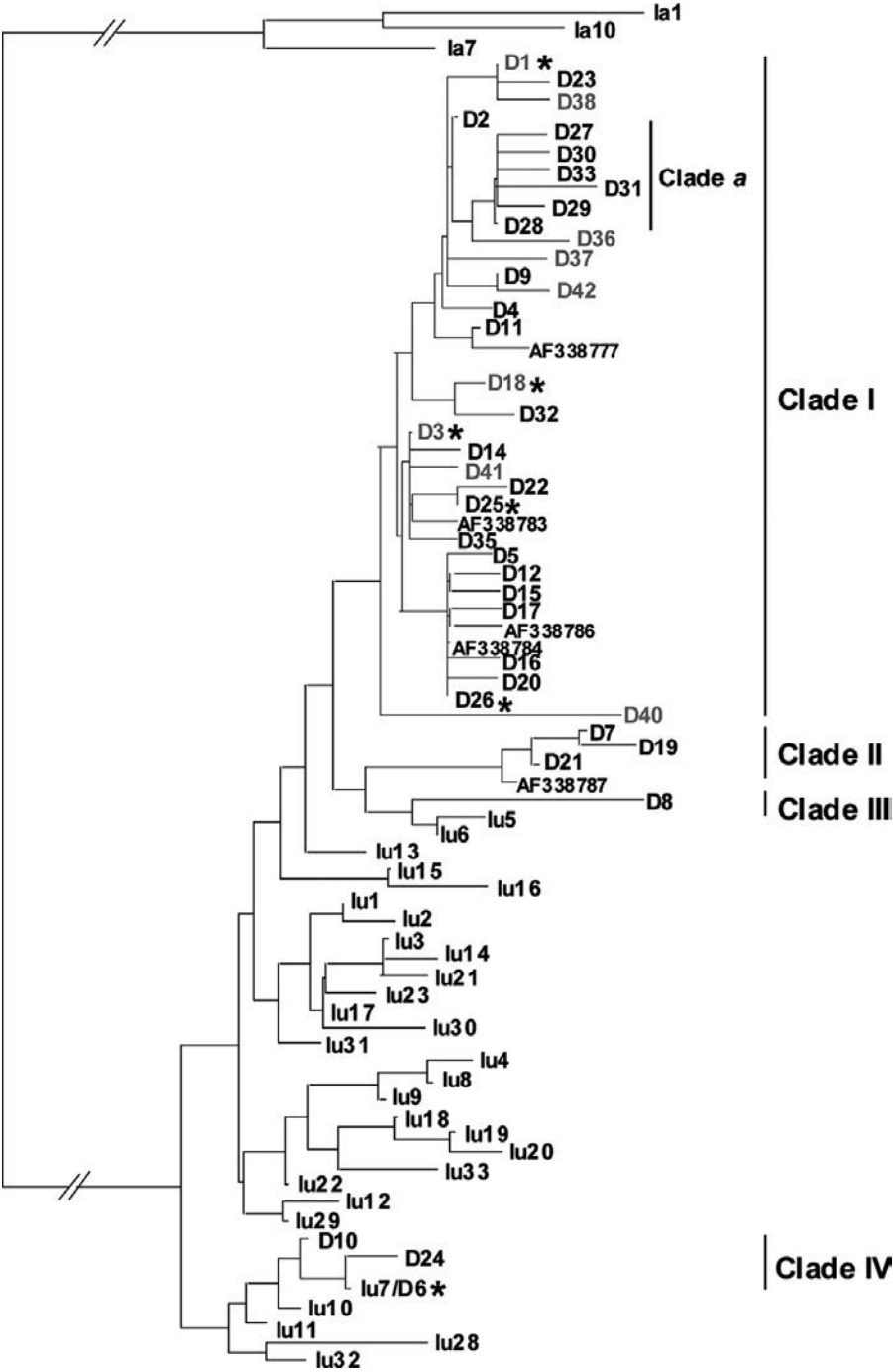


Figure 11.1. Neighbor-joining tree of wolf (W) and dog (D) mitochondrial DNA control region sequences (261 base pairs in length; Vilà *et al.* 1997). Dog haplotypes are grouped in four clades, I–IV (Vilà *et al.* 1999). Bold characters indicate haplotypes found in New World wolves (W20–W25). Modified from Vilà *et al.* (1999).

wolves. They often are smaller in body size and have wider crania, a more prominent facial stop, and a shortened, crowded jaw (Olsen 1985, Morey 1992). As the Asian wolves share traits with early dogs (i.e., small body size), the resulting implication was that Asian wolves are the direct ancestors of the dog (Olsen and Olsen 1977). However, a recent discovery identified the oldest known dog remains in western Russia and Belgium (Sablin and Khlopachev 2002, Germonpre *et al.* 2009), which do not show a reduction in body size when compared with the local population of gray wolves. These new remains suggests an early dog similar in size to the large European wolf, but having distinct differences in skull morphology unlike those previously reported. This difference implies that size and morphology are not dependable guides to the relationship between early dogs and wolves. Rather, skeletal differences between wolves and dogs may be a response to new selective pressures on proto-dogs related to co-existence with humans. Behavioral changes likely took place as well, such as increased docility and dependency on human handlers. In contrast, selection for specific phenotypic traits are unlikely to have directly caused changes to the mitochondrial DNA sequences used to understand the history of domestication. Thus, morphology and DNA sequences provide different information with regard to domestication, and discordance between them does not mean one or the other is flawed. Morphology provides direct information about the selective and cultural context of domestication, whereas DNA sequences provide information about population relationships and admixture.

3 The dog genome project and the canine mapping array

To date, over 2.5 million canine-specific single nucleotide polymorphisms (SNPs) have been identified and deposited in the public database as a result of the 7.5x Boxer genome sequencing effort (CanFam2.0, <http://www.broad.mit.edu/mammals/dog/snp/>; Lindblad-Toh *et al.* 2005). SNPs are simply nucleotide differences that are discovered (ascertained) by use of specific comparisons of sequences in a small panel of individuals. For the canine array, SNP ascertainment panels were used to maximize the genome-wide marker density and informativeness for gene-mapping studies in domestic dogs. The three major ascertainment schemes are as follows (Lindblad-Toh *et al.* 2005): (1) polymorphic in a comparison between two haplotypes of the Boxer genome; (2) polymorphic in a comparison between Boxer and Standard Poodle genome sequences; and (3) polymorphic in a comparison between Boxer sequence and low-coverage shotgun sequence reads from nine diverse dog breeds, four wolves (Alaskan, Chinese, Indian, and Spanish) and one coyote. Using this approach, more than 2.5 million SNPs have been detected, and a subset of 127,000 SNPs were used for the Affymetrix canine SNP array. SNP density on the array is approximately one SNP every 6kb, which equates to several SNPs per gene. On average, *c.* 72% of SNPs were polymorphic in a randomly chosen breed (Lindblad-Toh *et al.* 2005).

Thus, these SNPs are useful for genome-wide scans and fine-scale mapping within dog breeds and wolf populations.

4 Ascertainment bias

A major concern in SNP genotyping studies is the effect of ascertainment bias that results from SNP discovery using a narrow panel of individuals (see above). Because the ascertainment approach biases the collection of loci towards high-diversity SNPs and SNPs that segregate within particular lineages of dogs, the patterns of polymorphisms observed in other breeds and gray wolves will not be directly representative of SNP diversity. Further, if this bias varies substantially among regions of the genome, there can be spurious false signals of loci under selection. Correcting ascertainment bias is an active area of research (e.g., Nielsen *et al.* 2004, Clark *et al.* 2005, Novembre and Stephens 2008). The number of genome-sequenced vertebrates will increase dramatically over the next decade (Kohn *et al.* 2006) and consequently, analytical methods will improve as they are tested on a wider variety of species. In the following highlighted studies, ascertainment bias is addressed by separate analysis according to the three ascertainment schemes (see above) and the results were considered well supported if consistent across the ascertainment panels.

5 Analyses

5.1 Heterozygosity and diversity

Previous mtDNA sequence data suggest that East Asia was a center for dog domestication because sequence and haplotype variability is highest there (Savolainen *et al.* 2002). Consequently, we computed SNP heterozygosity based on different SNP ascertainment panels (Figure 11.2a,b; vonHoldt *et al.* 2010). We found that of the geographic groupings defined by Savolainen *et al.* (2002), only the small sample of African breeds in our study had substantially lower single-SNP heterozygosity (Figure 11.2a,b). This may reflect a bias of sampling purebred breeds since African village dogs have high mtDNA sequence and microsatellite variability (Boyko *et al.* 2009). Several aboriginal populations such as dingo, New Guinea Singing Dogs, and ancient breeds such as Basenji and Canaan dog have low heterozygosity and polymorphism (Figure 11.2a,b). The former are island populations and likely lost variation because of restricted founding events and subsequent small effective population sizes. Analysis of haplotype diversity shows the same basic patterns except that wolves clearly have greater variation than domestic dogs (Figure 11.2c). This reversal is likely due to the more limited effect of ascertainment bias on measures of haplotype diversity and suggests that haplotype diversity may be a more accurate indication of

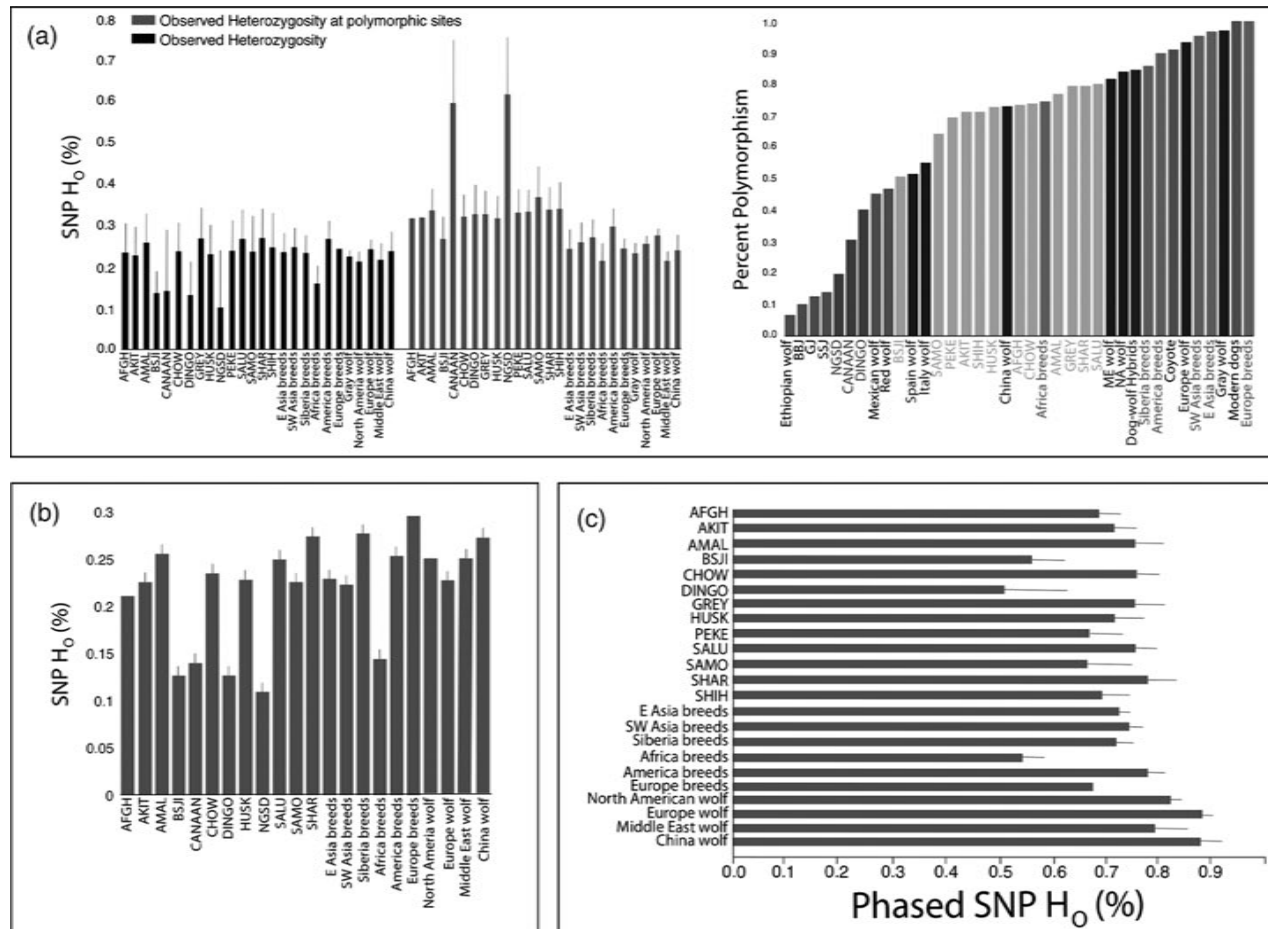


Figure 11.2. (a) Canine SNP microarray variation based on estimates of observed heterozygosity (H_O) for 48,036 SNPs and percent polymorphism for domestic dog breeds and breed groups (Savolainen *et al.* 2002), wolf populations, and canid species. (b) SNP-based estimates of observed heterozygosity for 546 SNPs ascertained from dog-wolf comparisons. (c) Observed heterozygosity (H_O) from phased genotype data. Note the higher values of heterozygosity in wolves vs. dogs as opposed to the opposite pattern in (a), suggesting the effect of ascertainment bias. Haplotype diversity estimates included breeds containing at least six individuals and wild canid populations for 500kb windows across the genome. Observed heterozygosity was estimated for 10-SNP non-overlapping windows across the genome. Modified from vonHoldt *et al.* (2010).

variation in populations (e.g., Reich *et al.* 2001). Finally, these basic results are supported by previous microsatellite analyses where no specific geographic area has lower variation (Parker *et al.* 2004). Our estimates of SNP heterozygosity and haplotype diversity, as well as previous microsatellite data, clearly do not support an East Asian origin for dogs and suggest multiple centers of origin or ancient backcrossing, or indicate a bias in mitochondrial DNA variation reflecting a higher rate of trade or higher dispersal of female than male dogs (Sundqvist *et al.* 2006).

5.2 Principal components and ADMIXTURE analyses

Principal components analysis (PCA) is often employed to simplify multivariate data and to reduce the dimensionality of genomic data (Novembre and Stephens 2008, Reich *et al.* 2008). Recently, PCA has revealed geographic gradients suggestive of recent demographic events, such as admixture or gene flow. However, the interpretation of PCA needs to be corroborated with independent analyses, such as Bayesian inference of subdivision, analysis of site frequency spectra, phylogenetic analysis, and demographic modeling. Currently, the popular software package EIGENSTRAT (Price *et al.* 2006, Bauchet *et al.* 2007) is employed to conduct PCA and correct for population subdivision when performing association testing. PCA is not specifically informative about the phylogenetic relationships among populations or species; rather, genomic trends on each principal component may be suggestive of recent demographic events.

To investigate the historical events during dog domestication, vonHoldt *et al.* (2010) used genome-wide SNP data from 155 gray wolves representing populations from Europe, the Middle East, North America, and Asia, and 912 unrelated dogs representing over 80 breeds registered with the American Kennel Club (AKC). Based on previous molecular analyses of domestic dogs, ancient and modern dog breeds were treated separately (Parker *et al.* 2004) and used to investigate the domestication process. PCA was performed for 48,036 high-quality SNP genotypes of dogs and wolves (Figure 11.3). The first principal component (PC1) explained 11% of the variation and reflected the separation of ancient dog breeds and wolves, whereas PC2 differentiated ancient breeds. For example, PC2 differentiated the East Asian and Indonesia breeds (i.e., Dingo and New Guinea Singing Dog) from Middle Eastern breeds (i.e., Afghan Hound and Basenji) (Figure 11.3). Our results dramatically demonstrate that dogs and wolves are genetically divergent, and that a deep genetic division exists between the ancient and modern breeds and between breeds from East Asia and the Middle East (Figure 11.3).

Genome-wide variation is expected to be spatially structured across geographically adjacent populations, and may be informative of recent admixture events. If adjacent wolf populations were used to augment ancient dog breeds, we would

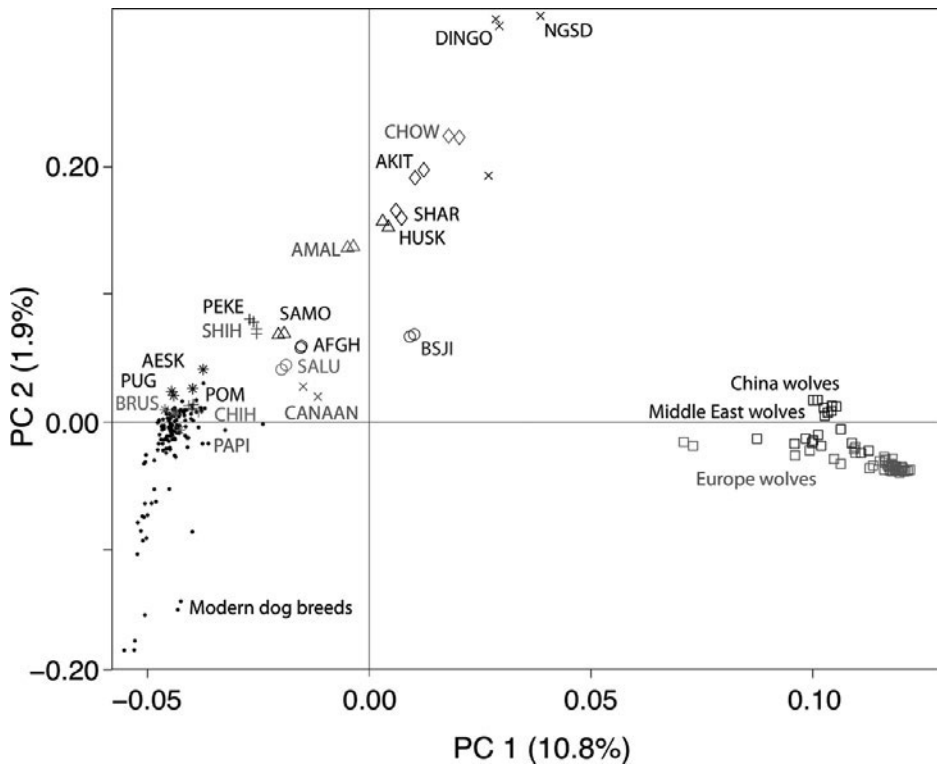


Figure 11.3. Principal components analysis of 171 dogs and 58 Eurasian wolves for 48,036 SNPs (Middle East wolf populations: India, Iran, Israel, Oman, Saudi Arabia, and Turkey). Modified from vonHoldt *et al.* (2010).

predict a signal of shared ancestry between those dog breeds and the corresponding wolf population. We analyzed population structure and ancestry with a new maximum-likelihood algorithm implemented in ADMIXTURE developed by Alexander *et al.* (2009). We used a data set of 43,954 unlinked loci that did not exclude SNPs if the correlation coefficient was high ($r^2 > 0.2$) among alleles. Twelve dogs representing each ancient dog breed and 58 Eurasian wolves were analyzed, assuming 2–6 ancestral populations ($K = 2$ to 6; Figure 11.4). Since dogs were not domesticated in North America, we excluded North American wolves from the analyses (Leonard *et al.* 2002). These results further support the genetic distinction between dogs and wolves as the primary genetic partition ($K = 2$) and secondarily, the differentiation of regional wolf populations ($K = 3$, Middle East, China, and Europe) and finally, of Middle Eastern (Afghan Hound, Basenji, Canaan dog, and Saluki) and East Asian dog breeds ($K = 4$, Akita, Chow-chow, Dingo, New Guinea Singing Dog, Shar-pei) (Figure 11.4). However, ancient breeds as a group always appear distinct and do not share an apparent genomic affiliation with any specific extant Old World wolf population.

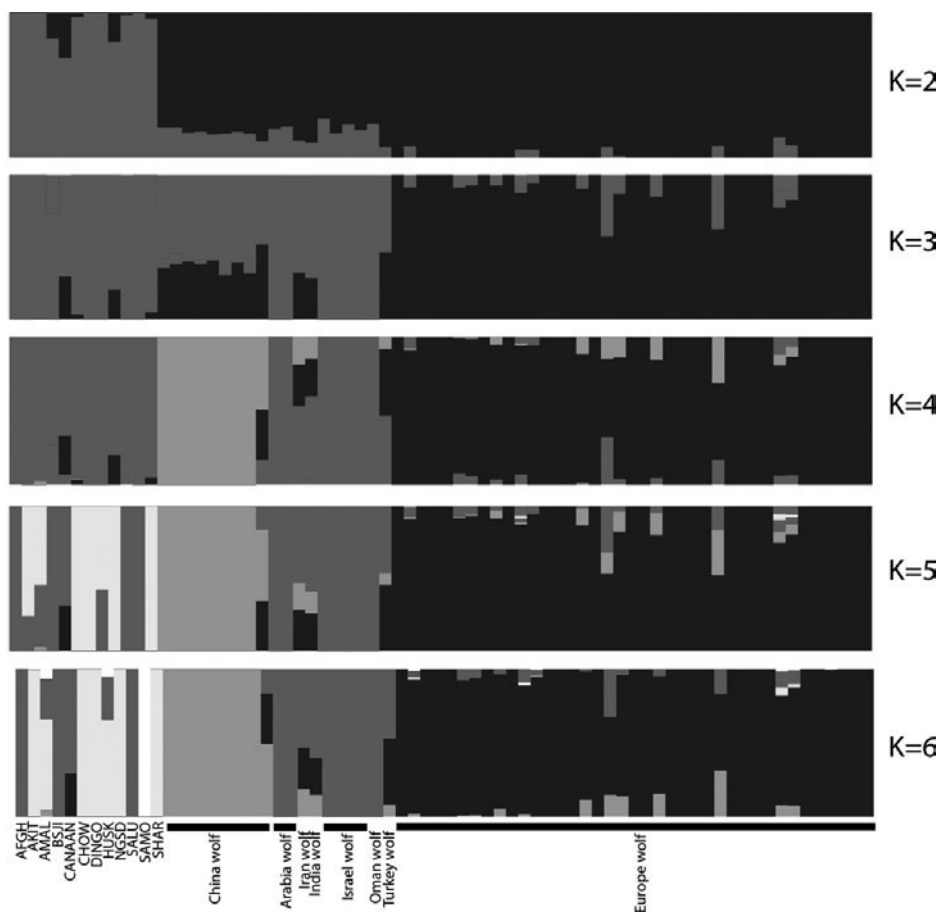


Figure 11.4. STRUCTURE analysis of ancient dog breeds (1 dog per breed) and 58 Eurasian wolves for 43,000 unlinked SNPs. The y-axis is the percent membership to each ancestral population and the x-axis is an individual multilocus genotype. (Dog breed abbreviations: Afghan Hound, AFGH; Akita, AKIT; Alaskan Malamute, AMAL; Basenji, BSJI; Canaan dog, CANAAN; Chow-chow, CHOW; Siberian Husky, HUSK; New Guinea Singing Dog, NGSD; Saluki, SALU; Samoyed, SAMO; Shar-pei, SHAR). Modified from vonHoldt *et al.* (2010).

5.3 Tree reconstruction

Tree reconstruction was based on single-locus SNP data and a pair-wise allele-sharing matrix, with similarity defined by identical-by-state (IBS) calculated using PLINK (Purcell *et al.* 2007). A neighbor-joining (distance-based) clustering algorithm based on allele sharing in the program POPULATIONS v1.2.3 (O. Langella, bioinformatics.org/~tryphon/populations/) for 43,954 unlinked high-quality SNPs of 574 dogs and wolves was constructed and rooted with the coyote. The consensus tree was generated in Phylip's CONSENSE program, and

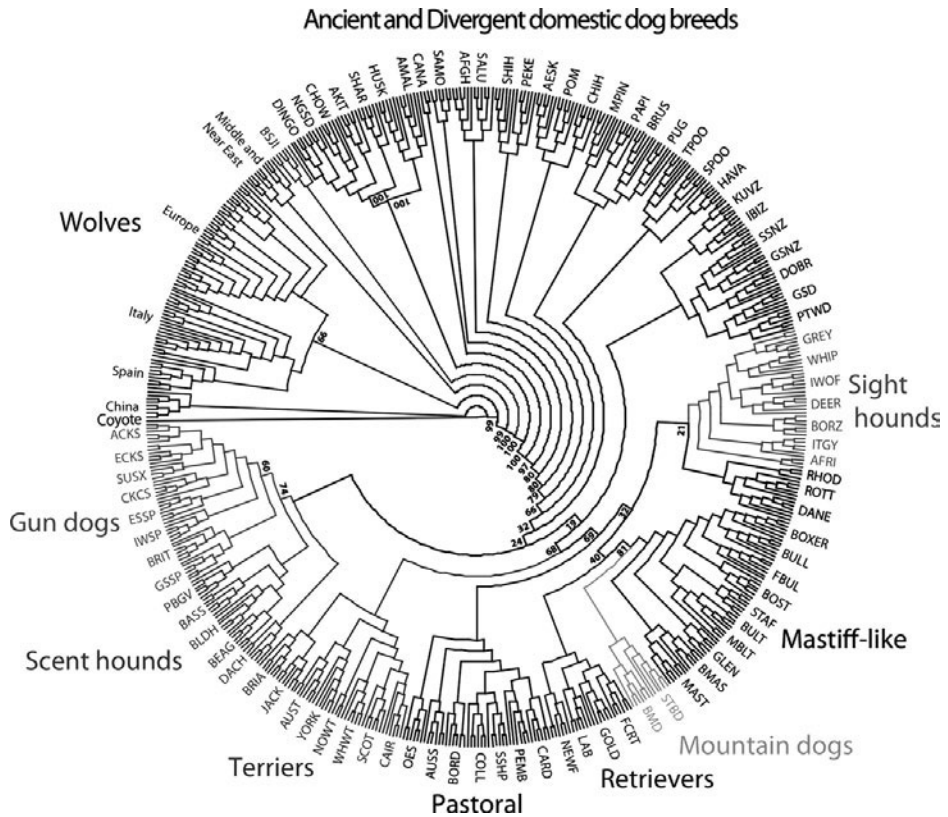


Figure 11.5. Neighbor-joining cladogram of 574 dogs and wolves, rooted with coyote data for 43,954 unlinked SNPs. Branch support for 1,000 bootstraps is indicated. Modified from vonHoldt *et al.* (2010).

1,000 re-sampling bootstraps were completed in SEQBOOT (Felsenstein 1993, Huson *et al.* 2007) (Figure 11.5). The tree clearly supports the partitions found in the PCA and ADMIXTURE analyses, such as the basic divisions between wolves and domestic dogs, and between dog breed groups. Further, the tree suggests that there are divisions between functional and phenotypic groups (i.e., sight, scent, retrievers, pastoral breeds) and implies these groups reflect actual genetic subdivisions among dogs. Moreover, there is a remarkable genealogical clustering of individuals within breeds. With one exception, all individuals in the tree cluster to their breed of origin, suggesting that breeds are highly differentiated units. Similar geographic clustering of wolves into their respective populations and more regional population groupings is also evident, corroborating previous results (Roy *et al.* 1994, Geffen *et al.* 2004, Fabbri *et al.* 2007, Musiani *et al.* 2007, Carmichael *et al.* 2008). Middle East wolves are found at the base of the divergence between dogs and wolves, implying that dogs either share an origin from Middle Eastern wolves or were genetically augmented by them early in domestication.

5.4 Haplotype sharing

In order to further resolve which wolf population most likely contributed to the genome of early domesticated dogs, vonHoldt *et al.* (2010) assessed the level of haplotype sharing among dog breeds and wolf populations (East Asia, Europe, and Middle East). Archaeological data suggest that domestication occurred in multiple locations (Europe, Middle East, East Siberia) but the mtDNA sequence data currently imply an East Asian origin (Olsen and Olsen 1977, Dayan 1994, Morey 1994, Nowak 2002, Sablin and Khlopachev 2002, Savolainen *et al.* 2002, Zeder *et al.* 2006, Germonpre *et al.* 2009). A problem with archaeological inference is the paucity of fossils and the inability to distinguish early dogs from wolves (see above, Germonpre *et al.* 2009).

Using the population program fastPHASE (Scheet and Stephens 2006), the chromosomal assignment of alleles for each SNP locus can be used for subsequent haplotype-based analyses. The chromosomes were partitioned into 2,634 windows each spanning 500kb and containing minimally 5–15 or >15 SNPs. Haplotype sharing was assessed from two permutation tests. The first test determined whether there was significantly more haplotype sharing with either Middle Eastern, European, or East Asian wolves for a given dog breed. The second permutation test assessed whether any of the four wolf populations (Middle Eastern, East Asian, European, or North American) significantly shared an excess of haplotypes with a dog breed.

From a total of 64 dog breeds and the 5–15 SNP windows, Middle Eastern wolves had highest sharing in all comparisons, with six breeds having significant sharing in at least one permutation test (Table 11.1). Similarly, for the >15 SNP windows, 75% (48/64) had highest sharing with Middle Eastern wolves, of which 38% (18/48) were significant for at least one test. The high degree of haplotype sharing among dog breeds and Middle Eastern wolves suggests an origin there, or as above, extensive backcrossing between Middle Eastern wolves and the ancestors of modern and ancient dog breeds. However, the similarity of some specific East Asian ancient breeds and Chinese wolves suggests that wolves from this area contributed to the dog genome as well (vonHoldt *et al.* 2010).

6 Resequencing and other SNP studies

Resequencing involves the sequencing of specific genomic regions in a population sample to discover novel genetic variants such as SNPs or insertion–deletion events. It is often done if preliminary association studies suggest that causative loci for specific phenotypes may exist in a specific area of the genome and there is some limited sequence data from the genomic locus. Additionally, resequencing data can be used to assess linkage disequilibrium (LD; the nonrandom association between alleles at different loci) that can be informative about a population's history (Gray *et al.* 2009). Further, the sequence information can be used to assess

Table 11.1. Permutation tests of haplotype sharing per breed with wolf populations

Only significant results are shown; bold indicates p -value < 0.05; asterisk indicates wolf population with the highest proportion of haplotypes shared with the dog breed.

Breed	5 to 15 SNP window				>15 SNP window			
	Highest haplotype sharing*	Haplotype explained (%)	Permutation Test 1	Permutation Test 2	Highest haplotype sharing*	Haplotype explained (%)	Permutation Test 1	Permutation Test 2
Afghan Hound	ME	0.3269	0.083	0.022	ME	0.306	0.056	0.104
Australian Terrier	ME	0.3324	0.038	0.028	EA	0.324	0.203	0.088
Basenji	ME	0.3734	0.019	0.001	ME	0.368	0.001	0.002
Basset Hound	ME	0.3071	0.243	0.206	ME	0.342	0.054	0.026
Borzoi	ME	0.3269	0.074	0.039	ME	0.341	0.06	0.023
Boxer	ME	0.3352	0.046	0.042	EA	0.359	0.139	0.079
Bullmastiff	ME	0.2978	0.314	0.29	EA	0.341	0.043	0.085
Chihuahua	ME	0.3138	0.14	0.088	ME	0.326	0.046	0.026
Flat-coated Retriever	ME	0.3113	0.218	0.155	ME	0.339	0.036	0.041
German Short-haired Pointer	ME	0.3107	0.164	0.097	ME	0.325	0.04	0.098
Greyhound	ME	0.3119	0.18	0.142	EA	0.347	0.339	0.035
Irish Water Spaniel	ME	0.307	0.175	0.156	ME	0.353	0.006	0.007
Kuvasz	ME	0.3112	0.193	0.107	ME	0.348	0.015	0.003
Labrador Retriever	ME	0.3138	0.13	0.131	ME	0.337	0.032	0.096

Table 11.1. (cont.)

Breed	5 to 15 SNP window				>15 SNP window			
	Highest haplotype sharing*	Haplotype explained (%)	Permutation Test 1	Permutation Test 2	Highest haplotype sharing*	Haplotype explained (%)	Permutation Test 1	Permutation Test 2
Miniature Pinscher	ME	0.3197	0.169	0.087	EA	0.334	0.068	0.031
Pekingese	ME	0.3162	0.199	0.085	ME	0.338	0.03	0.013
Pomeranian	ME	0.3034	0.205	0.188	ME	0.326	0.04	0.122
Portuguese Water dog	ME	0.3197	0.101	0.099	NA	0	0.039	0.976
Pug	ME	0.3115	0.259	0.208	ME	0.362	0.012	0.007
Rottweiler	ME	0.3157	0.137	0.144	ME	0.348	0.037	0.064
Saluki	ME	0.3342	0.041	0.013	ME	0.32	0.045	0.055
Shetland Sheepdog	ME	0.3121	0.199	0.131	ME	0.361	0.049	0.052
Siberian Husky	ME	0.2939	0.495	0.215	ME	0.305	0.082	0.016
English Springer Spaniel	ME	0.3036	0.254	0.174	ME	0.3397	0.036	0.042
Staffordshire Terrier	ME	0.3166	0.135	0.103	EA	0.3807	0.774	0.01
Standard Poodle	ME	0.3073	0.163	0.129	ME	0.3627	0.003	0.023
Whippet	ME	0.3184	0.107	0.1	EA	0.3532	0.068	0.038

population relationships as shown in a DNA sequence tree or in a PCA analysis as above. An important advantage of using resequencing data only is that ascertainment bias is not an issue because all individuals have been sequenced for the entire genomic region. A disadvantage of resequencing data, however, is that it requires more sequencing effort, a problem that may be reduced with the recent availability of next-generation sequencing technologies (Binladen *et al.* 2007, Hodges *et al.* 2007). Below we use a hybrid approach by first defining SNPs through sequencing of a large discovery panel and then typing those SNPs in population sampling of wolves and dogs.

6.1 Resequencing of five genomic regions

Recombination, recurrent mutation, selection, admixture, and mate choice are factors that influence the extent of LD within a species (Gaut and Long 2003, Mueller and Andreoli 2004, Deonier *et al.* 2005). Among populations of the same species that share similar rates of recombination and mutation, and where selection is weak, a critical variable for determining the extent of LD is demographic history. In general, populations that have remained large for a substantial period of time or have rapidly expanded demonstrate lower levels of LD than those that are small or have experienced recent population bottlenecks (Pritchard and Przeworski 2001, Reich *et al.* 2001, Gaut and Long 2003, Mueller and Andreoli 2004). To explore the relationship of LD and demographic history in dogs using SNP data ascertained in a fashion different from that on the canine SNP array, 5 regions on 5 chromosomes (1, 2, 3, 34, 37) were resequenced, each including a noncontiguous 5Mb span (Gray *et al.* 2009). The initial panel included 5 breeds of dog ($n = 97$) with further sequencing of 4 wolf populations ($n = 73$), and one coyote population ($n = 17$). Genotyping of 106 of the dog-discovered SNPs was then carried out across a larger sample of 18 dog breeds ($n = 546$; unrelated at the grandparent level), 14 gray wolf populations ($n = 344$), one coyote population, ($n = 18$), and 4 other wild canid populations ($n = 93$). Similar to vonHoldt *et al.* (2010), principal component analysis of the genotype data confirmed the differentiation of domestic dogs from other wild canids and showed a slight overlap only with gray wolves along PC1 and PC2 (Figure 11.6). Old World and New World wolves were observed to have a slight separation along PC1 with most Old World wolves appearing spatially closer to domestic dogs than New World wolves. Although, minimal overlap was observed between several dogs and wolves, Akita, an ancient breed, displayed the most distinct separation. Akita was divergent from the main cluster of dogs and overlapped slightly with Old World wolves, several of which were wolves from Israel (Figure 11.6). While the general trend of dog/wolf separation was as observed in vonHoldt *et al.* (2010), the study by Gray *et al.* (2009) did not observe the tight clustering of breeds. This difference is likely due to the number of SNP loci studied, which is greatly reduced from that in vonHoldt *et al.* (2010).

From genotype and sequence data, considerable variation in the extent of LD across breeds of dog was observed and ranged from *c.* 20 kb in breeds with

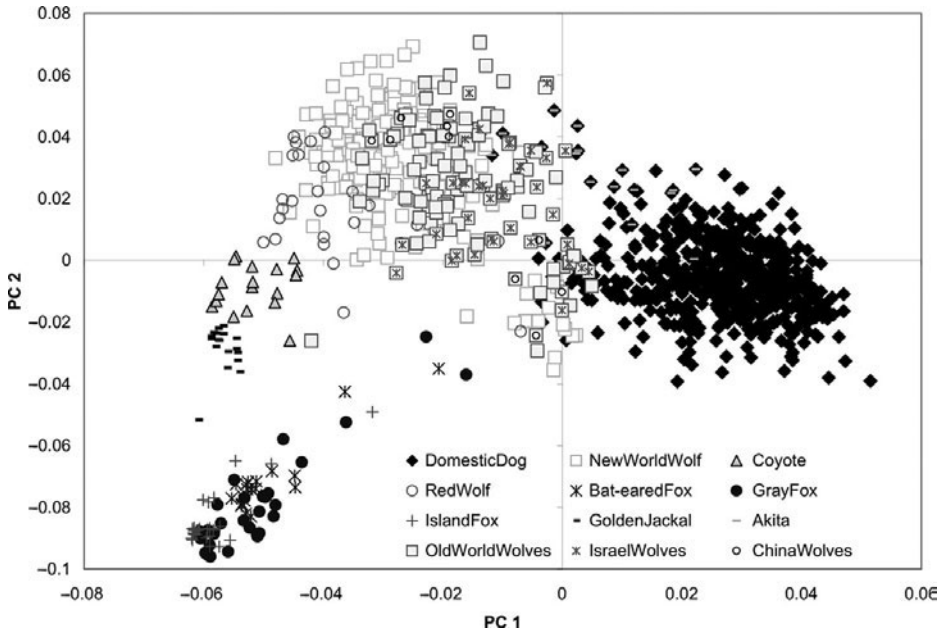


Figure 11.6. Principal components analysis of 106 SNP (dog-derived) genotypes from 18 dog breeds, 14 gray wolf populations, one coyote population, and 4 other wild canid populations. Modified from Gray *et al.* (2009).

large population sizes to >5 Mb in breeds that have experienced significant bottlenecks or had remained small in size (Sutter *et al.* 2004, Gray *et al.* 2009). This large range in the extent of LD paralleled that observed in 11 gray wolf populations and one coyote population where LD varied from <10 kb in large outbreeding populations to >1.7 Mb in small or recently bottlenecked populations. However, wolves overall had lower levels of LD. A significant correlation was found between LD and the number of AKC registered individuals (Kendal's τ , p -value = 0.003; Mantel's test, p -value = 0.0002) (Figure 11.7). These results strongly suggest LD in the dog is associated with population size and breeds with high LD may have been founded recently or remained at small size for long time periods. For example, the Labrador Retriever showed levels of LD closest to that seen in outbreeding gray wolf populations. This finding likely reflects the popularity and large breeding population of the breed, with $\sim 150,000$ new registrations in the USA per year (<http://www.akc.org/>), whereas the Mastiff has a smaller breeding population with $\sim 7,000$ new registrations per year and more extensive LD (Gray *et al.* 2009). Composite-likelihood modeling of the resequenced data found that only a 5% reduction in nucleotide diversity was observed as a result of domestication, whereas the loss of nucleotide diversity with breed formation averaged 35% (Gray *et al.* 2009). Consequently, the original bottleneck associated with domestication was relatively minor compared to that associated with breed formation. This result is consistent with the high

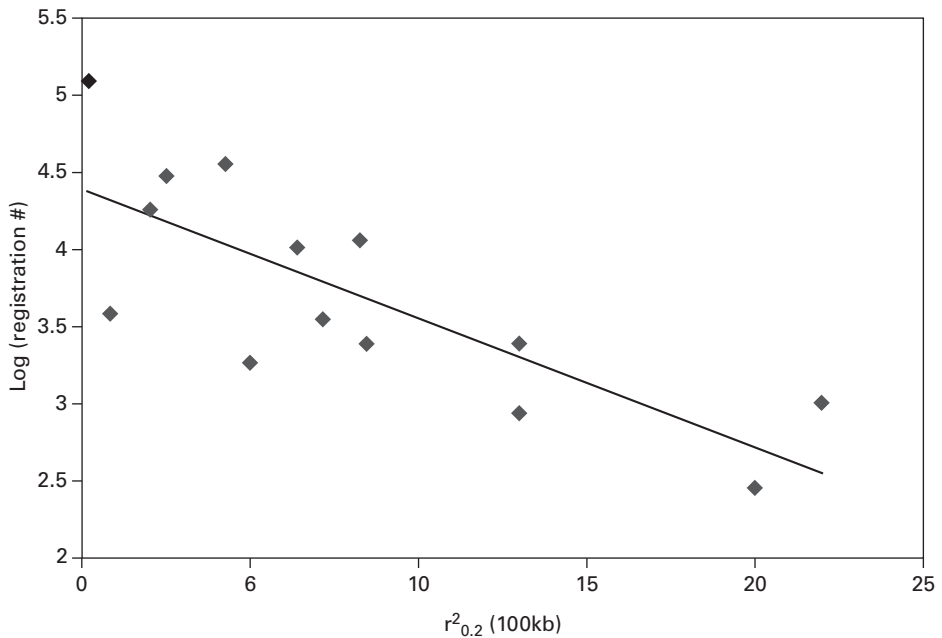


Figure 11.7. Correlation between the extent of LD and the log of the number of AKC registered individuals for 14 dog breeds. Modified from Gray *et al.* (2009).

diversity of SNPs, MHC alleles, and mitochondrial DNA haplotypes among dog breeds compared to that within breeds (Vilà *et al.* 1999, 2005, vonHoldt *et al.* 2010).

6.2 Resequencing of *IGF-1*

The genomic region containing the insulin growth factor-1 (*IGF-1*) gene is implicated as a primary gene for body size differences in domestic dogs (Sutter *et al.* 2007). A variant of *IGF-1* that evolved early in the history of dogs was fixed in small dog breeds and may have been the keystone mutation from which size diversity evolved. Resequencing of the exons of *IGF-1* did not yield any nonsynonymous mutations that would affect the structure of the resulting protein; however, sequencing of the intronic regions identified a single SNP marker and antisense retrotransposon (SINEC_Cf) located in intron 2 as being most proximate to the causal mutation (Sutter *et al.* 2007). Gray *et al.* (2010) explored the evolutionary history of the *IGF-1* gene further by resequencing and genotyping key markers in the intron 2 region across a global sampling of gray wolf populations. They did not find the small body size SNP allele nor the antisense retrotransposon in any of the 17 gray wolf populations ($n = 374$) examined. Neighbor-joining trees were constructed from 4,811 bp and 6,331 bp of sequence from 14 gray wolf populations ($n = 20$) and 8 small and large dog breeds ($n = 10$). Gray *et al.* observed small dog breeds to cluster with wolves

from Israel, Iran, and India with 68% bootstrap support out of 1,000 to 10,000 bootstrap resamplings (Figure 11.8). Large domestic dog breeds clustered with all other gray wolves and had a bootstrap support of 75% and 94% (4,811bp and 6,331bp, respectively). To verify the tree topology, they constructed constraint trees in which the “small dog” haplotype was constrained to clusters containing the “large dog” haplotypes. Maximum likelihood analysis of the constraint trees confirmed that the likelihoods of the unconstrained trees were significantly better (p -value <0.001 in all cases). Thus, these results demonstrate that all small dogs have a unique SNP allele and SINE element suggesting an early evolution of small size in dogs and providing support for their Middle Eastern origin.

7 Summary and conclusions

We demonstrate the use of extensive genome-wide SNP data from the canine genotyping array and from resequencing studies to resolve relationships of dogs to each other and to their wild progenitor populations. We show that, with the exception of African breeds, no specific geographic population of dogs has lower variation, suggesting that multiple centers of origination and ancient backcrossing or trade have influenced current patterns of variation. We then analyze relationships of dogs and wolves using tools appropriate to SNP data. First, we apply principal components analysis, which is an assumption-free approach to display genome-wide data for large population samples. Second, we utilize an ADMIXTURE model that groups individuals into genetic partitions in approximate Hardy–Weinberg equilibrium. Third, we demonstrate that simple tree clustering methods provide a straightforward heuristic tool for displaying relationship between groups. Lastly, we consider levels of haplotype sharing that demonstrate a single dominant genomic signature of specific wolf ancestry in domestic dog breeds. The conclusions from these analyses are further supported by SNP data that have been independently ascertained. Specifically, we used data from 106 SNPs originating from resequencing data of five genomic regions in a limited panel of dogs and wolves. These data provide support of those conclusions based on the canine genotyping array. Lastly, we phylogenetically analyzed direct sequencing data from wolves and dogs near the *IGF-I* gene, thus providing three distinct genomic perspectives on dog origins and relationships.

The results of these analyses demonstrate clustering on three levels. First, we find that all individuals are clustered to their breed of origin. This nearly absolute genealogical concordance reflects a narrow breed founding, small effective population size, and genetic isolation. Dog breeds often originate from the crossing of individuals from different breeds or from mutational “sports” which are then backcrossed to littermates. Subsequently, effective population sizes are often small because of the “popular sire effect” whereby a small number of males, especially champions, are used to fertilize a large number of females (Parker and Ostrander 2005). Also, population size varies among breeds, and we show that

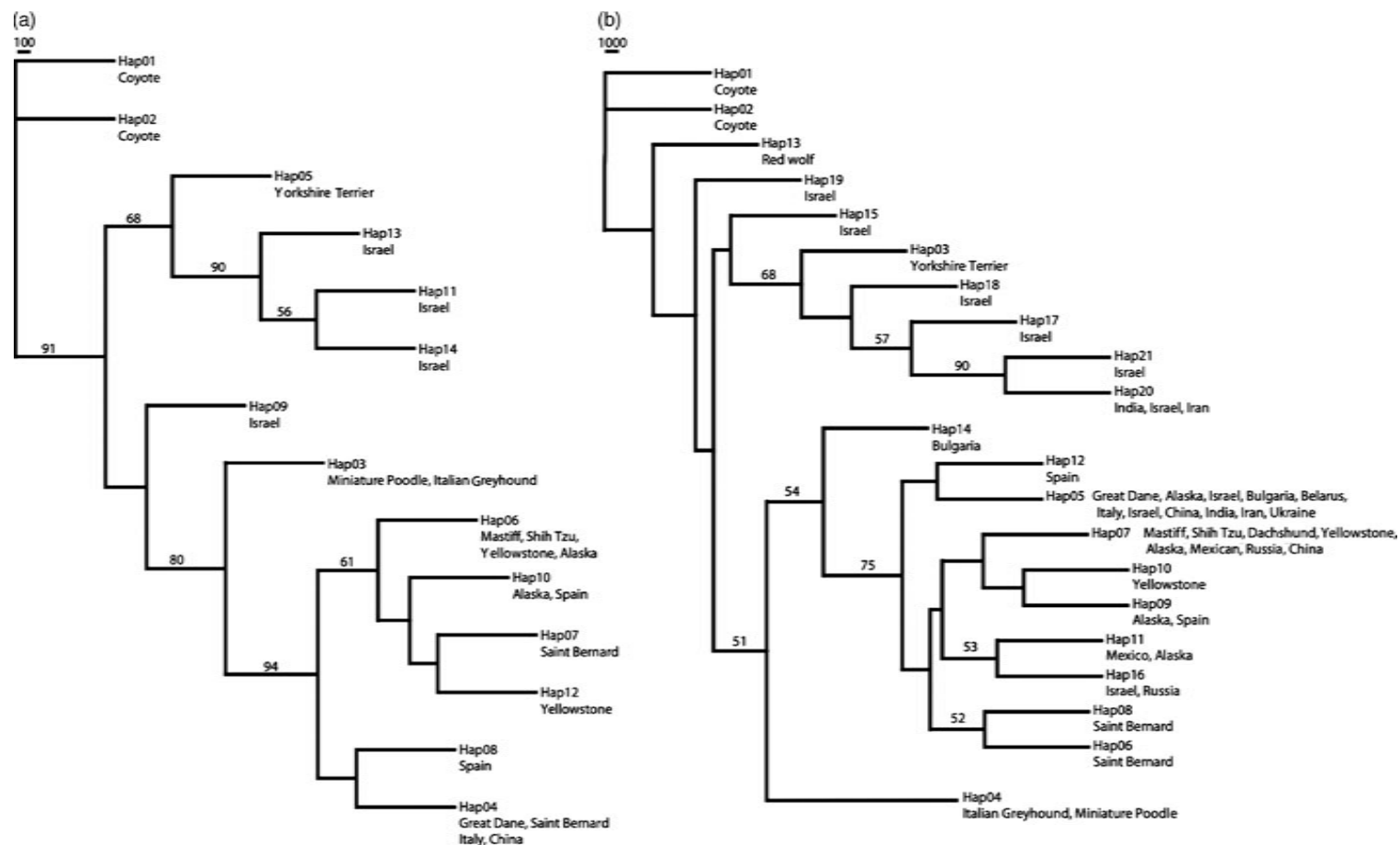


Figure 11.8. *IGF-1* intron 2 neighbor-joining tree based on: (a) 6,331bp (1,000 bootstraps) and (b) 4,811bps (10,000 bootstraps) of DNA sequence. Support values below 50% not shown. Modified from Gray *et al.* (2010).

LD is highly correlated with the number of individuals registered with a breed. Second, we show through a clustering analysis that several functional and phenotypic breeds cluster in distinct groups. These clusters are evident within the radiation of modern dog breeds and suggest that new breeds generally form from other breeds that are similar in phenotype or function. For example, retriever breeds may serve as a source through crossing of distinct breeds that also retrieve well and thus define a related group of dogs. Similarly, there appears to be a tendency for breeds that have a terrier phenotype to be bred as founders for new dog breeds, which are then genetically assigned to the same breed group.

A basic partition within dogs is between ancient and modern breeds. The ancient breeds define long-diverged lineages that appear to be dominantly Middle Eastern and East Asian in origin. However, there are some unexpected ancient breeds, such as the Spitz breeds (i.e., Siberian Husky and Alaskan Malamute). The existence of these two distinct ancient lineages suggests a long-term persistence of dogs in both areas, and the potential for independent domestication or backcrossing with wolf populations. However, the haplotype-sharing analysis suggests that the dominant influence on the dog genome derives from Middle Eastern wolves. This implies that the common ancestral population of dogs were wolves from the Middle East and that early in domestication ancient dogs were isolated in East Asia and potentially interbred with native wolves there. Consequently, ancient East Asian breeds remain highly diverged from modern dog breeds, which are the results of selective breeding beginning in the Victorian era. Finally, our results suggest that dogs and wolves are highly divergent gene pools that should be considered distinct species. The nearly absolute discrimination of the two species implies that despite some backcrossing early on in the history of domestication, dogs otherwise have been genetically isolated from wolves.

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12 Malaria and Rickets Represent Selective Forces for the Convergent Evolution of Adult Lactase Persistence

Loren Cordain, Matthew S. Hickey, and Kami Kim

Most of the world's adults cannot drink milk without digestive disturbances because the gut enzyme lactase-phlorizin hydrolase (LPH), responsible for hydrolyzing lactose into easily digestible glucose and galactose, does not persist long after weaning. Notable exceptions to this global generalization are most northern Europeans and certain African and Bedouin pastoralists with high rates of adult lactase persistence (ALP) (Swallow 2003). Accordingly, it is commonly accepted that the high prevalence of ALP in these populations arose rapidly by selection for the LPH encoding gene (*LCT*) in the 5,000 to 10,000 years since their adoption of dairying (Swallow 2003, Bersaglieri *et al.* 2004, Tishkoff *et al.* 2006). Clearly, gene flow from dairying populations with pre-existing high rates of ALP may underlie intermediate ALP frequencies in societies with no history of dairying. Nevertheless, the ability to digest milk is considered an archetypal example of gene-culture co-evolution whereby dairying confers selective benefit to those adults who can drink milk ad libitum without digestive discomfort. The selection coefficient (*s*) for putative *LCT* alleles in sub-Saharan Africans (0.035 to 0.097) (Tishkoff *et al.* 2006), Europeans (0.014 to 0.15) (Bersaglieri *et al.* 2004), and Scandinavians (0.09 to 0.19) (Bersaglieri *et al.* 2004) has been labeled: (1) “among the strongest yet seen for any gene in the genome” (Bersaglieri *et al.* 2004) and (2) “one of the strongest genetic signatures of natural selection yet reported in humans” (Tishkoff *et al.* 2006).

In Europeans, a single nucleotide polymorphism, C/T-13910, is most frequently related to persistence or nonpersistence of LPH, because presence of the T-13910 allele is highly (86%–98%) associated with ALP (Poulter *et al.* 2003, Högenauer *et al.* 2005, Ridefelt and Hakansson 2005) and, in vitro, promotes binding of the *LCT* transcription factor, Oct-1 (Lewinsky *et al.* 2005). In contrast, T-13910 is either absent or present at low frequencies (0%–14%) in sub-Saharan African and Bedouin milk-drinking pastoralists with ALP (Mulcare *et al.* 2004, Ingram *et al.* 2007). An exception to this general trend is the sub-Saharan Fulani people, who maintain a high incidence of T-13910, likely due to a degree of

Caucasian admixture in their gene pool (Enattah *et al.* 2007). A number of candidate alleles for *LCT* regulatory mutations in sub-Saharan African pastoralists include G-13907, G-13915, and C-14010 (Tishkoff *et al.* 2006), although G-13915 abolishes rather than enhances Oct-1 binding (Ingram *et al.* 2007). Hence, the presence of T-13910 likely represents the genetic basis for ALP in most northern Europeans, but not in most sub-Saharan Africans and Bedouins. Consistent with these observations is the conclusion that ALP arose independently and multiple times throughout human history from at least two or more LPH-promoting alleles, which conferred a powerful selective advantage (Coelho *et al.* 2005).

Many studies have concluded that the selective advantage for ALP stemmed from the additional nutritional benefits (energy, carbohydrate, fat, protein, water, and calcium) accrued from the ad libitum consumption of milk without gastrointestinal discomfort (Simoons 1970, Bersaglieri *et al.* 2004, Tishkoff *et al.* 2006). Given the abrupt rise of T-13910 in Scandinavian and European populations (beginning 54–106 and 267–300 generations ago, respectively) (Bersaglieri *et al.* 2004) and the independent precipitous rise of other putative LPH-encoding alleles in sub-Saharan Africans (beginning 90 to 227 generations ago) (Tishkoff *et al.* 2006), it is unlikely that this powerful selective pressure for separate LPH coding alleles originated entirely from the simple, additive food calories supplied by milk (Gibson 2007). Rather, additional properties of high milk consumption must have attenuated certain environmental elements that were previously responsible for high mortality in these independent populations.

We demonstrate that the primary selective advantage for the strong and rapid assimilation of ALP genes in sub-Saharan Africans arose, not necessarily because it allowed for digestion of milk's added calories or water, but more importantly because it reduced malarial mortality. In contrast, the selection for ALP-encoding genes in northern Europeans attenuated mortality from rickets; a potentially lethal disease in Neolithic farmers caused by high cereal consumption and compromised sunlight exposure at northerly latitudes.

1 Adult lactase persistence and malaria

An extensive literature review by Kretschmar and Voller (1973) and by Nowell (1970) has demonstrated that exclusive milk diets suppress malarial infections in birds, rodents, and primates by severely restricting *p*-aminobenzoic acid (PABA) intake. The suppression of malarial symptoms is abrogated when supplemental PABA is added to all milk or PABA-deficient diets of infected animals (Nowell 1970, Kicska *et al.* 2003). In addition to its minimal PABA content, bovine milk is also a poor source of folate, averaging 6–9 µg per 100g (Johnston *et al.* 2002) relative to the daily recommended intake (DRI) of 400 µg. Although *Plasmodia* species can synthesize folate de novo via the Shikimate pathway (Figure 12.1), recent data indicate that these parasites cannot synthesize sufficient quantities to

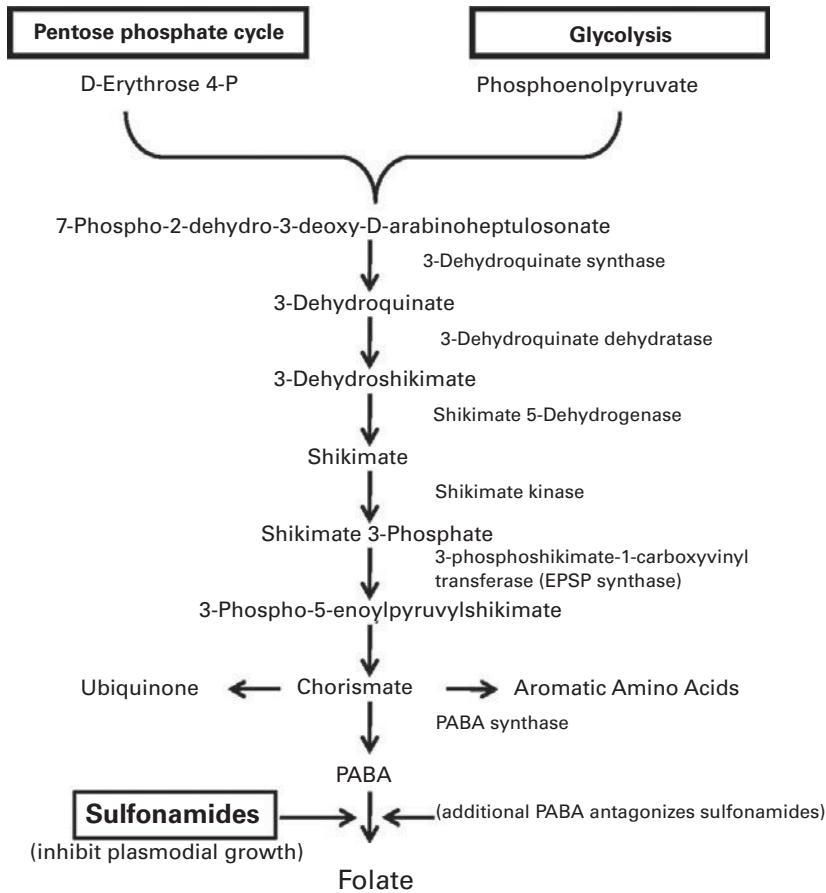


Figure 12.1. The biosynthetic Shikimate pathway and its branches. Adapted from Elandalloussi *et al.* 2005.

survive in vivo (Kicska *et al.* 2003). Because PABA, pterin, and glutamate moieties are required for the de novo synthesis of folate in bacteria, then dietary-induced deficiencies of PABA and folate induced by high milk diets may suppress malarial symptoms by impairing folate metabolism in *Plasmodia* species. In support of this notion are rodent models of malaria demonstrating that both dietary PABA and folate reduce the efficacy of sulfa drugs (Jacobs 1964).

The pastoralist Fulani exhibit a well-established resistance to malaria compared to other nonmilk-drinking African sympatric ethnic groups that is unexplained by known genetic resistance factors (Modiano *et al.* 1996), but rather by enhanced immunity (Bereczky *et al.* 2006). Displacement of PABA- and folate-rich foods by milk may attenuate malaria infection while allowing immune exposure, serving to prevent serious sequelae and facilitate the establishment of protective immunity. In this regard, the high prevalence of ALP (68% of the population) (Swallow 2003) in the Fulani may represent a previously unrecognized genetic factor that indirectly reduces malarial mortality.

Human populations in malaria-endemic areas have been subject to strong selective pressure for traits that confer protection to malaria. These traits include hemoglobinopathies and other mutations that affect erythrocyte longevity such as G6PD deficiency (Tishkoff *et al.* 2001). Selection for ALP may have been prevented by the prevalence of animal trypanosomiasis, which precludes widespread cattle husbandry in much of Africa. Nonetheless, in high malarial regions where ALP is widespread, reduced dietary PABA intake caused by high milk consumption may disrupt the life cycle of *Plasmodia* species by impairing folate metabolism, thereby reducing childhood malaria fatalities and overall morbidity within adults.

2 Adult lactase persistence and rickets

Because malaria is and was rare or absent in northern Europe (Hay *et al.* 2004), the rapid assimilation of LPH encoding alleles in these populations following the introduction of agriculture occurred from other selective pressures. Although the prevalence of ALP in Europeans is frequently described as occurring in a northwest to southeast gradient with highest frequencies in the northwest (Swallow 2003), a more accurate description is the concentric distribution portrayed in Figure 12.2 (Beja-Pereira *et al.* 2003). The highest ALP frequencies appear in populations residing within *c.* 1000 km of the North and Baltic Seas and living at high latitudes (*c.* 53 to 58° N). The circum-Baltic/North Seas region is one of the few high-latitude regions in the world where cereal grains can be successfully grown without intensive modern agricultural procedures. Normally, at high latitudes, extreme temperatures cause the growing season to be too fleeting for cereal crops to effectively compete with animal foods as a staple. Because the warm Gulf Stream flows into the North and Baltic Seas and because of the nearness to a maritime heat sink (Seager 2006), temperatures in the surrounding landscapes were warm enough to allow Neolithic farmers to successfully grow cereals as staples (primarily wheat and barley).

The combination of high cereal consumption and compromised sunlight exposure at high latitudes produced an environment highly conducive for developing rickets. High-cereal diets have been routinely used to induce rickets in animals (Mellanby 1919, Thomas and Steenbock 1936, Grammer *et al.* 1983) including primates (Sly *et al.* 1984). Epidemiological studies of human populations consuming high intakes of unleavened bread show rickets and vitamin D deficiency to be widespread (Hunt *et al.* 1976, Brooke *et al.* 1981, Gibson *et al.* 1987). Whole cereals are rachitogenic because their high fiber content impairs the entero-hepatic circulation of vitamin D, leading to increased fecal elimination of 25-hydroxyvitamin D₃, thereby progressively lowering plasma 25-hydroxyvitamin D₃ concentrations in humans (Batchelor and Compston 1983). Moreover, whole grains are poor sources of calcium, and their high phytate content impairs calcium absorption and additionally contributes to their rachitogenicity (Cordain 1999). For cereal-dependent

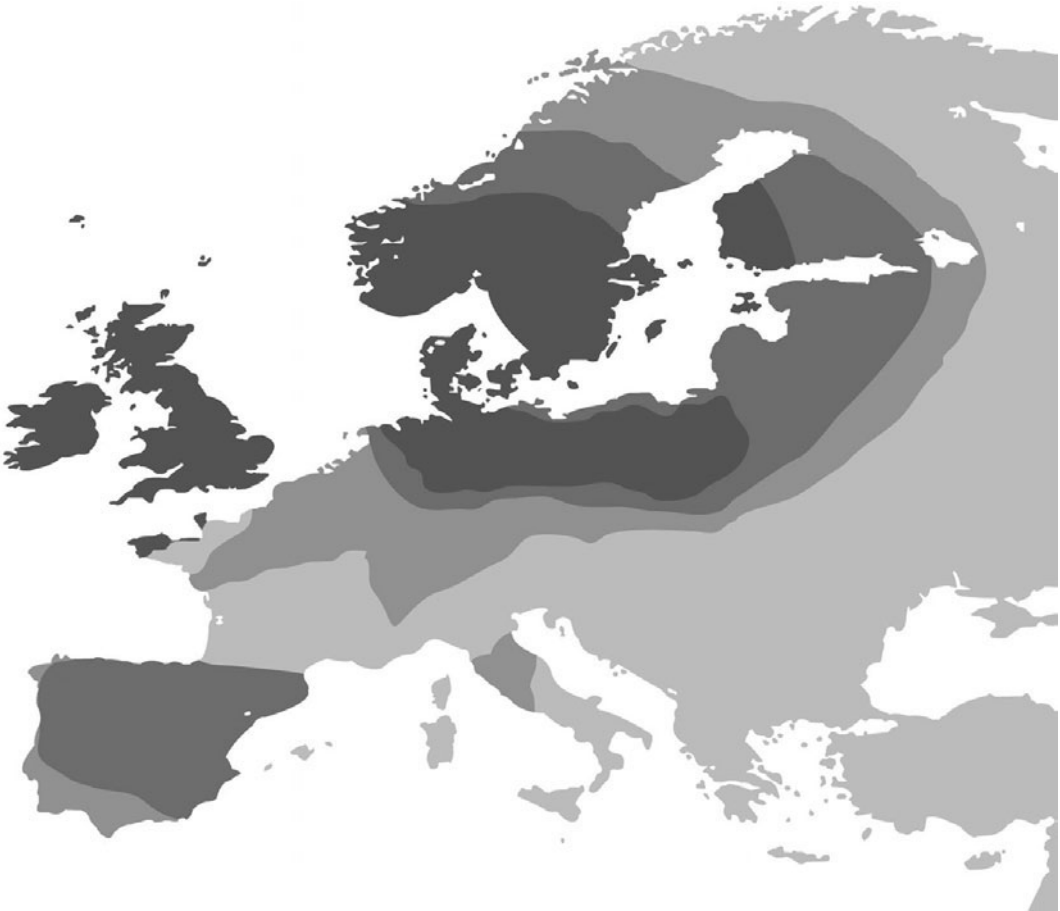


Figure 12.2. The geographic distribution of the adult lactase persistence allele in contemporary Europeans. The darker the color, the higher the frequency of the adult lactase persistence allele. Adapted from Beja-Pereira *et al.* 2003.

Neolithic populations of the circum-Baltic/North Seas areas, vitamin D status would have been further compromised from the reduced sunlight at high latitudes and the inherent lack of ultraviolet radiation necessary for epidermal vitamin D synthesis.

Although rickets is rarely fatal in children and adolescents, it may cause pelvic flattening in adult females, thereby permanently narrowing the birth canal (Osmanov 1987) and greatly increasing maternal mortality during childbirth (Loudon 1986). In sixteenth to eighteenth century England, estimated maternal mortality was 24–29 deaths per 1,000 births, with significant mortality directly attributable to rickets (Loudon 1986). Under the more primitive birthing conditions of the Neolithic, maternal mortality likely was higher still. Consequently, the reliance upon whole grains and the reduced ultraviolet radiation in high-latitude Neolithic farmers represented powerful negative selective pressures



Figure 12.3. The geographic distribution of hair and eye pigmentation in contemporary Europeans. The lighter the color, the lighter is hair and eye pigmentation. Adapted from Cavalli-Sforza *et al.* 1994.

producing estimated mortality rates (mother and fetus) similar to malarial mortality in sub-Saharan African children (6.23 per 1,000 children) (Snow *et al.* 1999). The selection for LPH alleles and the ad libitum consumption of milk without gastrointestinal distress in circum-Baltic/North Seas farmers would have been protective against rickets by milk's high calcium content, which operates independently from vitamin D to prevent nutritional rickets from cereal-based diets (Pettifor 2004).

The simultaneous selection for extreme dermal depigmentation along with ALP in circum-Baltic/North Seas Neolithic farmers would have further protected against rickets by enhancing epidermal vitamin D synthesis (Jablonski and Chaplin 2000). Geographic variation in pigmentation indicates the world's lightest hair color and irises (Figure 12.3) (Cavalli-Sforza *et al.* 1994) and skin complexions (Figure 12.4) (Brace 2000) are native to a similar circum-Baltic/North Sea region as ALP. The arrival of dairying and cereal crops to the circum-Baltic/Norths region occurred approximately 5,000–6,000 years ago (Zohary and Hopf 2000) which coincides with the estimated origins of extreme dermal depigmentation (5,300–6,000 years ago) (Gibbons 2007, Norton *et al.* 2007), blue irises (6,000–12,000 years ago) (Eiberg *et al.* 2008), and ALP (5,000–12,000 years ago) (Enattah *et al.* 2007). These data support the notion that ALP, fair complexions, light hair and blue irises spread uniquely and simultaneously in the circum-Baltic/North Seas region to counter the negative selection pressure of rickets brought on by the introduction of cereal grains to a sunlight-compromised environment.

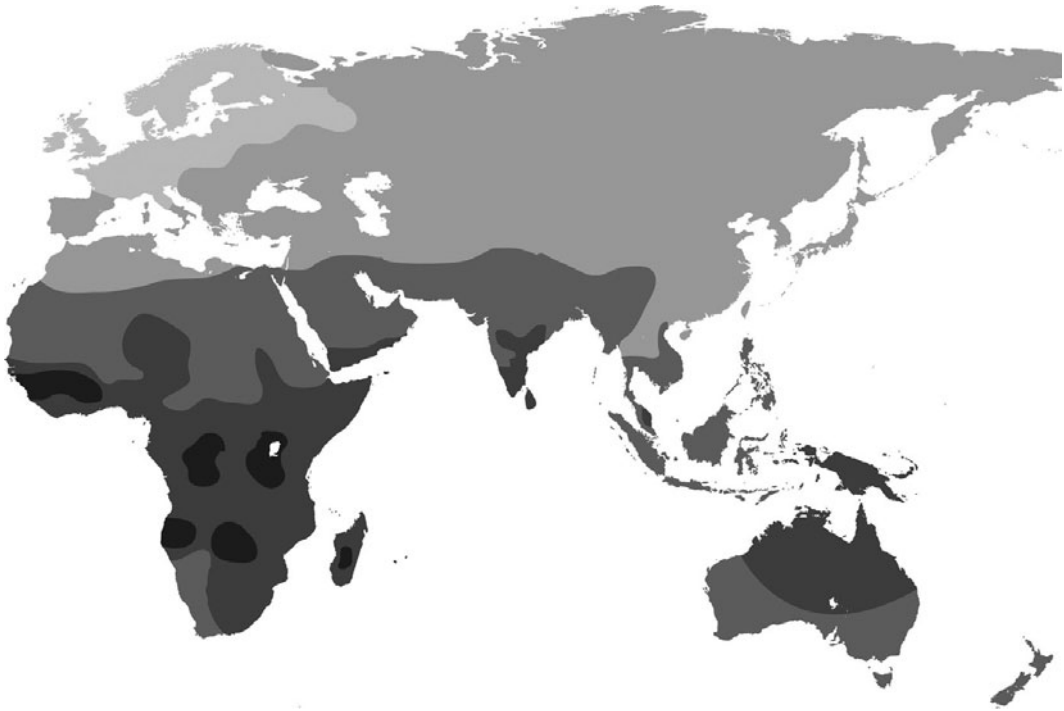


Figure 12.4. The Old World geographic distribution for dermal pigmentation. The lighter the color, the lighter the skin pigmentation. Adapted from Brace 2000.

3

Summary

Our analysis suggests that ALP arose independently in sub-Saharan pastoralists and northern Europeans from discrete selective pressures: malaria and rickets, respectively. In circum-Baltic/North Sea Europeans the combined pressures of high-cereal diets and reduced ultraviolet radiation simultaneously triggered the rapid selection for ALP and extreme dermal depigmentation – two evolutionary adaptations that would have reduced rickets mortality.

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Section III

Issues in Plant Domestication

Paul Gepts

The four contributions in this section illustrate the domestication continuum across time and space. While domestication started in specific areas (variously called centers of agricultural origins or domestication or even Vavilovian centers), it is now conducted outside these original areas as well. Likewise, domestication started roughly 10,000 years ago in association with the end of the last ice age, and is still practiced today by farmers and breeders. Each stage and location of agricultural development represents potentially different evolutionary factors that can shape the domesticated gene pools. Dissemination from the original hearths of agriculture undoubtedly brought into the picture factors such as selection for adaptation to new environments as well as genetic drift due to small sample sizes. Different cultivation areas also reflect different human cultural environments and, hence, distinct cultivation and consumption requirements.

More specifically, the first two chapters – McCouch *et al.* ([Chapter 13](#)) and Chacón *et al.* ([Chapter 14](#)) – address the origin of domestication of rice and lima bean, respectively, and document the two main domestications that have taken place several millennia ago in these two crops. In contrast, the latter two chapters address contemporary study and use of crop genetic resources: Veasey *et al.* ([Chapter 15](#)) on two important native root crops (cassava and yam) as managed by farmers in Brazil, and Gowda *et al.* ([Chapter 16](#)) on pigeonpea breeding.

McCouch *et al.* ([Chapter 13](#)) document the contrasting results on Asian rice (*Oryza sativa*) domestication obtained with either anonymous molecular markers or domestication gene DNA sequences. The former confirm the existence of two major domesticated gene pools, *indica* and *japonica* (including the temperate and tropical *japonicas*), and identifies two additional subdivisions – the *aus* and *aromatics*, which are more closely allied with the *indicas* and *japonicas*, respectively. This picture of fairly marked divergence among groups is in contrast with the information provided by sequence analysis of individual domestication genes. The latter suggests that a sizable group of domestication alleles were first selected in the *japonica* group and subsequently introduced into the *indica* group.

This contrasting information allows the authors to propose a more complex domestication process that takes into account potential gene flow between wild and cultivated populations and so-called *proto-indica* and *proto-japonica* populations. Many aspects of this new picture remain to be clarified such as a potential geographic divergence, if any, within the *Oryza rufipogon* ancestral species and the dynamics of outcrossing and gene flow between different groups.

In [Chapter 14](#), Chacón *et al.* also discuss the origin of domestication of a crop – lima bean (*Phaseolus lunatus*) – with two domestications. Initially, lima bean was thought to have been domesticated once and to consist of three cultivar groups with a distinct geographic spread and distribution in Mesoamerica and northern South America. Further explorations leading to additional populations of wild and domesticated lima beans, as well as the application of a wide range of molecular markers, has led to a different view of the domestication process of this species. The current view posits a double domestication, one in the Andes and the other in an as yet undetermined area in Mesoamerica, leading to a larger-seeded and smaller-seeded gene pool, respectively.

In their analyses of two native root crops – cassava and yam – in Brazil, Veasey *et al.* ([Chapter 15](#)) show how socio-cultural and economic contexts, in addition to biological and ecological ones, influence the genetic make-up of farmer seed stocks. The two species have distinct genetic systems. Cassava is a diploid species, with a mixed vegetative–sexual reproductive system. Yam, in this case, is a polyploid, dioecious species. In general, yams are used more in subsistence systems, whereas cassava is more integrated in a market economy. The differences between these two species are reflected in the distribution between and within fields. In yams, there is greater divergence between swidden fields within communities, reflecting different preferences of households.

Finally, [Chapter 16](#) by Gowda *et al.* illustrates how breeders have adopted pigeonpea and modified it from a partly domesticated crop into a fully domesticated one. Initial domestication steps had modified the perennial life history into an annual one, had reduced seed dormancy, and had increased the harvest index. To further increase productivity, breeders further increased earliness to Extra-Short-Duration (ESD) lines and harvest index. They reduced photoperiod and temperature sensitivity to broaden adaptation and are exploring the use of cytoplasmic male sterility to facilitate the development of hybrid cultivars.

Overall, these four chapters show how innovative approaches can help us understand the origins of domestication of crops, but also the effect of contemporary selection both by farmers and breeders. The efforts outlined here will play an increasingly important role in conserving crucial biodiversity, which is increasingly threatened by habitat destruction and global warming.

13 The Dynamics of Rice Domestication: A Balance between Gene Flow and Genetic Isolation

Susan R. McCouch, Michael J. Kovach, Megan Sweeney, Hui Jiang, and Mande Semon

The relationship between domesticated crop species and their wild ancestors has fascinated geneticists and evolutionists for over 150 years (Darwin 1859, 1868). Over the past century, growing awareness of the value of plant genetic diversity has led to global efforts to preserve genetic resources (Vavilov 1926, Plucknett *et al.* 1983, Chang 1984, Plucknett 1987, Harlan 1992). More recently, tools for investigating genetic diversity and evolution at the molecular level have provided new opportunities to investigate the process of crop domestication and to more efficiently utilize natural variation in crop improvement (Tanksley and McCouch 1997, Hoisington *et al.* 1999, Wing *et al.* 2005, Doebley *et al.* 2006, Dubcovsky and Dvorak 2007, Johal *et al.* 2008).

1 Domestication

Over the course of domestication, plant species undergo a series of profound phenotypic changes that result from human selection on diverse, wild populations. The genetic changes responsible for the suite of traits that differentiate domesticated plants from their wild ancestors are referred to as the “domestication syndrome” (Hammer 1984). These may include nondehiscence or non-shattering (lack of seed dispersal at maturity), more compact growth habit, reduction in seed dormancy, enhanced size and yield of edible plant parts, reduced toxicity, and changes in the reproductive system, generally toward increased rates of self-pollination or vegetative propagation (Simmonds 1979, Gepts 2004). Plants may be cultivated for hundreds or thousands of years before they are domesticated; until a plant has been modified to the extent that it can no longer survive without human intervention in its natural environment, it is not considered completely domesticated. The domestication of plants and animals had a profound impact on the structure and interactions of human societies. Most notably, humans transitioned from hunting–gathering to agriculture as the main

form of food acquisition, allowing them to live sedentary lives and introducing the potential for food surpluses, population expansion, occupational specialization, and social stratification.

Domestication of crop species from their respective wild relatives occurred independently in multiple parts of the world at different points over the course of human history. In some cases, the timing and location of the domestication process is fairly well documented, as in the case of maize (Matsuoka *et al.* 2002), wheat (Heun *et al.* 1997, Dvorak *et al.* 1998, Ozkan *et al.* 2005, Dubcovsky and Dvorak 2007, Luo *et al.* 2007), common bean (Piperno and Dillehay 2008, Kwak and Gepts 2009, Kwak *et al.* 2009), or sunflower (Burke *et al.* 2002, 2005), while for other crops, the details of the domestication process are still being investigated.

2 The genus *Oryza*

Oryza is a small but complex genus consisting of two cultivated and 22 wild species (Vaughan 1994, Ge *et al.* 1999). The wild species can be grouped into ten genome types based on molecular, morphological, and cytological studies, namely AA, BB, CC, BBCC, CCDD, EE, FF, GG, HHJJ, and HHKK (Ge *et al.* 1999). Molecular clock data suggests that diversification of the genus *Oryza* occurred 8 to 14 Mya (Guo and Ge 2005).

There are both wild and cultivated species having the AA genome. Often referred to as the *Oryza sativa* complex, the AA genome group is the most recently diverged lineage in the genus, having diversified approximately 2 Mya (Ma and Bennetzen 2004, Zhu and Ge 2005). In addition to the two domesticates, *O. sativa* and *O. glaberrima*, from Asia and W. Africa, respectively, the *O. sativa* complex is comprised of six wild diploid species. These include the Asian ancestors of *O. sativa*, *O. rufipogon* Griff. (perennial) and *O. nivara* Sharma et Shastri (annual), the African ancestor of *O. glaberrima*, *O. barthii* (annual), the African perennial species, *O. longistaminata*, the Australian annual *O. meridionalis*, and the South American annual–perennial species, *O. glumaepatula* (Vaughan 1989, 1994). All members of the AA genome are sexually compatible and molecular studies provide evidence of abundant episodes of hybridization and introgression among them (Semon *et al.* 2005, Zhu and Ge 2005, Tang *et al.* 2006).

3 A-genome species diversity

3.1 Asian wild rice

O. rufipogon (perennial) and *O. nivara* (annual) are traditionally referred to as separate species based on morphological and life-history differences (Nayar 1973, Vaughan 1989). However, a lack of reproductive isolation, coupled with evidence of continuous variation between these species, substantiates the conclusion

that they should be treated as members of the same species (Sano *et al.* 1980, Barbier *et al.* 1991, Lu *et al.* 2002, Zhu and Ge 2005, Zhu *et al.* 2007). This conclusion is consistent with the views of Oka (1988) and Morishima *et al.* (1992), who viewed them as distinct ecotypes of the *O. rufipogon* complex (Oka 1988, Morishima *et al.* 1992, Zhu and Ge 2005). For the purposes of this chapter, both *O. rufipogon* and *O. nivara* will be referred to as *O. rufipogon*.

Studies of *O. rufipogon* genetic diversity have identified numerous subpopulations within the species that show evidence of geographic and ecological differentiation (Sun *et al.* 2001, Zhu and Ge 2005, Londo *et al.* 2006, Wang *et al.* 2008). Despite this evidence, it is difficult to distinguish ancestry from introgression in *O. rufipogon*, due to the high level of admixture with *O. sativa* documented for this outcrossing species (Ge *et al.* 1999, Chen *et al.* 2004). Populations of *O. rufipogon* from China harbor greater genetic variation than wild populations found in South or SE Asia (Gao and Hong 2000, Sun *et al.* 2001, Zhou *et al.* 2003). When levels of diversity within populations are compared, wild populations collected in southern China have higher levels of genetic diversity than populations from more northern areas of China (Zhou *et al.* 2003, Wang *et al.* 2008).

When the mean diversity of *O. rufipogon* is compared to that of *O. sativa*, the cultivar is estimated to contain between 22% and 77% of the genetic variation detected in its wild ancestor, depending on the polymorphism assay used and the germplasm evaluated (Sun *et al.* 2001, Londo *et al.* 2006, Caicedo *et al.* 2007, Gao and Innan 2008). The relative intensity of the domestication bottleneck in *O. sativa* is estimated to be slightly greater than that of maize, an outcrossing species (Caicedo *et al.* 2007, Gao and Innan 2008), but less than that of hexaploid wheat (Buckler *et al.* 2001, Dubcovsky and Dvorak 2007, Haudry *et al.* 2007).

3.2 African A-genome wild rice

There are two wild AA-genome species native to Africa, the annual *O. barthii* and the perennial *O. longistaminata*. The relationship between these two taxa is very different from that described above for *O. nivara* and *O. rufipogon*. *O. longistaminata* is the most genetically divergent of the A-genome species and is difficult to cross with other A-genome relatives (Ghesquiere 1987), while *O. barthii* is the undisputed progenitor of African cultivated rice, *O. glaberrima*. *O. barthii* is less genetically diverse than *O. rufipogon*, and similarly *O. glaberrima* contains significantly lower levels of genetic diversity than *O. sativa* (Second 1982, Ishii *et al.* 2001, Semon *et al.* 2005). Depending on the marker system used, *O. barthii* and *O. glaberrima* occasionally cluster more closely with *O. longistaminata* than with the Asian A-genome species (Joshi *et al.* 2000, Kwon *et al.* 2006), but using intronic sequence from four nuclear genes, *O. barthii* was shown to be more closely related to its Asian cousin *O. rufipogon* than to its nearest neighbor, *O. longistaminata* (Zhu and Ge 2005).

Table 13.1. The recognized subpopulations of *Oryza sativa*

Group ID	Subpopulation	Varietal group	Reference
Group I	<i>indica</i>	<i>Indica</i>	Glaszmann 1987, Garris <i>et al.</i> 2005
Group II	<i>aus</i>	<i>Indica</i>	Glaszmann 1987, Garris <i>et al.</i> 2005
Group III	<i>deep water</i>	<i>Indica</i>	Glaszmann 1987
Group IV	<i>rayada</i>	<i>Indica</i>	Glaszmann 1987
Group V	<i>aromatic</i>	<i>Japonica</i>	Glaszmann 1987, Garris <i>et al.</i> 2005
Group VI	<i>temperate japonica</i>	<i>Japonica</i>	Garris <i>et al.</i> 2005
Group VII	<i>tropical japonica</i>	<i>Japonica</i>	Garris <i>et al.</i> 2005

4 Subpopulation structure within *O. sativa*

Two major varietal groups within *O. sativa* have been recognized since ancient times. In China, these are referred to as *hsien* (*indica*) and *keng* (*japonica*) (Chou 1948, Chang 1976, Second 1982, Oka 1988, Wang and Tanksley 1989). These two major groups can be further subdivided into several ecotypes or genetic subpopulations using isozyme and DNA markers (Glaszmann 1987, Garris *et al.* 2005, Caicedo *et al.* 2007, Zhao *et al.* 2010, 2011). Based on 15 isozyme markers, Glaszmann (1987) recognized six genetically differentiated subpopulations, including two rare ecotypes found only in a limited area within modern-day Bangladesh and northeastern India (Groups III and IV, Table 13.1). In a subsequent study by Garris *et al.* (2005), the subpopulation structure of *O. sativa* was refined based on SSR and chloroplast markers and the groups recognized by SSR analysis were later confirmed by SNP analysis (Caicedo *et al.* 2007, Zhao *et al.* 2010, 2011).

As summarized in Table 13.1, a total of seven genetic subpopulations of *O. sativa* have now been identified using all three marker systems. (Note: the isozyme classification did not differentiate between *temperate* and *tropical japonica*, so these groups were collectively referred to as Group VI by Glaszmann (1987)). SSR analysis indicated that 37.5% of the variation identified in *O. sativa* corresponded to differences among groups (F_{ST} values), while the remaining 62.5% was attributable to diversity within groups. Groups I, II, III, and IV are recognized as members of the *Indica* varietal group, while chloroplast analysis and pairwise F_{ST} values suggest that Groups V, VI, and VII are closely related to each other in the *Japonica* varietal group (Garris *et al.* 2005).

Plant breeders have traditionally recognized the same subpopulations of *O. sativa* based on morphological characteristics, flowering time, geographic distribution, ecological adaptation, and sterility barriers (Oka 1988, Khush 1997), but the genetic relationships among the groups were not previously well understood. What is most surprising to many plant breeders is the close relationship between Group V (the *aromatic* subpopulation, which contains the *Basmati* and *Sadhri* varieties) and the *Japonica* varietal group. It has long been assumed that the Group V subpopulation was more closely related to *Indica* due to the long, slender

grain morphology that is shared by many (but not all) Group V and Group I varieties (Ali *et al.* 2011), and the fact that both are widely grown in South Asia (Maqbool *et al.* 1998, Bashir *et al.* 2004). Also, despite the significant genetic divergence between the Group I (*indica*) and Group II (*aus*) subpopulations ($F_{ST} = 0.26$), these groups are often lumped together due to the paucity of morphological features that distinguish them.

5 Subpopulation structure within *O. glaberrima*

O. glaberrima was domesticated more recently than *O. sativa*, and estimates suggest that this occurred in West Africa approximately 3,500 years ago (Viguier 1939). Using SSRs, three cryptic subpopulations were identified within *O. glaberrima*, as well as an admixed group that contained a high proportion of *O. sativa* ancestry (Semon *et al.* 2005). Admixed accessions were most abundant in countries lying along the mouths of the Casamance and Cacheo Rivers (Sierra Leone, Guinea Conakry, Liberia, Senegal, and Guinea Bissau) where *O. sativa* was first introduced into West Africa by Portuguese navigators in the fifteenth to seventeenth centuries. Approximately 67% of the 198 *O. glaberrima* accessions showed evidence of some admixture with *O. sativa* despite the fact that admixed types were not easily distinguished at the phenotypic level from native accessions of *O. glaberrima*. This is consistent with the fact that *O. glaberrima* and *O. sativa* are often grown in mixed stands throughout West Africa today.

The three subpopulations identified in *O. glaberrima* are not as well differentiated as the subpopulations of *O. sativa*. Only 14% of the SSR variation detected by Semon *et al.* (2005) corresponded to differences among the three indigenous groups of African rice, compared to 37.5% among the five subpopulations identified in *O. sativa*. This is consistent with a more recent domestication of *O. glaberrima* from its wild ancestor and a more intense domestication bottleneck. While the study found no evidence of isolation by distance among *O. glaberrima* subpopulations, the subpopulation structure was significantly correlated with phenotypic characters indicative of ecological differentiation (Semon *et al.* 2005). Overall, the relationship between SSR variation, phenotypic characters, geographical distribution, and ecological adaptation was consistent with the history of domestication as described by Portères (1970) and underscores the impact of human activity on the population substructure observed in domesticated crop species.

6 The domestication of Asian rice

The process of rice domestication in Asia continues to be a subject of debate. This debate revolves around the question of whether *O. sativa* was domesticated from a single population of *O. rufipogon*, with subsequent, rapid divergence into the respective *O. sativa* subpopulations (Morishima *et al.* 1963, Chang 1976, Oka

1988, Lu *et al.* 2002), or whether the *Indica* and *Japonica* varietal groups were domesticated independently from a genetically pre-differentiated ancestor (Chou 1948, Second 1982, Sun *et al.* 1997, Cheng *et al.* 2003, Zhu and Ge 2005, Kawakami *et al.* 2007). A second level of discussion revolves around the question of whether proto-*Indica* and proto-*Japonica* populations of *O. rufipogon* existed as distinct, geographically isolated populations (Khush *et al.* 2003, Vitte *et al.* 2004, Londo *et al.* 2006), or whether pre-differentiated ancestral populations occupied ecologically differentiated but geographically overlapping zones (Vaughan *et al.* 2008, Zeng *et al.* 2003, Zhou *et al.* 2003, Zhang *et al.* 2007).

The fact that there has been continuous gene flow within and between cultivated and wild rice over the past 10,000 years and that human trade, migration, and population expansion have moved populations of both *O. sativa* and *O. rufipogon* back and forth across Asia makes it difficult to sort out the complex evolutionary dynamics that gave rise to the modern subpopulations of *O. sativa*.

The rapid accumulation of information about specific genes associated with domestication provides an opportunity to address questions about single versus multiple origins and to trace the way domestication alleles have moved both genetically and geographically from one subpopulation to another across the vast expanse of Asia (Kovach *et al.* 2007, Shomura *et al.* 2008). As new domestication-related genes are cloned and characterized, and their distributions in different varietal groups, geographies, ecologies, and cultural groups are documented, we gain new insights into the relative timing of mutations associated with the domestication syndrome, the subpopulations in which they arose and how they were subsequently accumulated into early *O. sativa* landraces.

7

Cloned genes related to rice domestication and varietal differentiation

Several key genes associated with rice domestication and varietal identity have recently been cloned in rice. These include *grain shattering 4*, *SH4* (Li *et al.* 2006), *grain shattering 1*, *SH1* (Konishi *et al.* 2006), *red pericarp*, *Rc* (Sweeney *et al.* 2006), *grain size 3*, *GS3* (Fan *et al.* 2006), *grain incomplete filling 1*, *GIF1* (Wang *et al.* 2008), *seed width 5*, *SW5* (Shomura *et al.* 2008), *prostrate growth habit 1*, *PROG1* (Jin *et al.* 2008, Tan *et al.* 2008), and *waxy*, *WX* (Yamanaka *et al.* 2004). Only a few of these genes have been characterized with respect to their origins and distribution in the different subpopulations, but interesting patterns are emerging as this information becomes available.

In this chapter, we review the information that is currently available regarding the genetic origins and dispersal of alleles associated with domestication and varietal identity in rice and highlight some observations that help us address questions about the complex process of domestication in *O. sativa*. It should be noted that much recent research aimed at cloning domestication genes and surveying the frequency of the domestication alleles has focused on Chinese rice accessions, and this may currently bias conclusions about the relative importance

of these alleles and the evolutionary history of this crop. Nevertheless, a study of haplotype diversity around these putative domestication genes provides reasonably objective evidence that can be used to trace the genetic origin and subsequent dissemination of alleles if a broadly representative panel of rice germplasm is used for the analyses. Additional efforts to identify and characterize domestication alleles from diverse accessions originating in under-represented parts of the rice-growing world are needed to ensure that our understanding of the domestication syndrome in rice is based on an unbiased sample of genetic resources and domestication-related genes.

7.1 *Shattering 4 (SH4)*

The *Shattering 4 (SH4)* gene is a putative transcription factor that is involved in cell wall degradation and establishment of the abscission layer that causes the grain to disassociate from the panicle (Li *et al.* 2006). The functional mutation causing shattering was identified as a single nucleotide polymorphism at the RY-repeat *cis* element affecting the DNA-binding domain of the gene. The nonshattering mutation at this locus (*sh4*) was identical in a panel of over 200 *Indica* and *Japonica* rice accessions examined, suggesting a common origin for this trait in the two varietal groups (Li *et al.* 2006, Lin *et al.* 2007). These results could mean that the *sh4* allele arose and was selected before the differentiation of *Indica* and *Japonica* from a common *O. rufipogon* ancestor, as suggested by Lin *et al.* (2007), or it could be concluded that the *sh4* allele was selected very early during domestication of one of the *O. sativa* subpopulations and was subsequently introduced into other rice populations. There is no clear evidence at this time that can resolve which of these scenarios is most likely. However, the importance of this trait for domestication and the ubiquitous occurrence of the mutation in all *O. sativa* cultivars examined suggest that it occurred early in the domestication process. This was presumably at a time when rice was still largely outcrossing such that introgressive hybridization between cultivated (but not yet fully domesticated) and neighboring wild populations would have been a common occurrence. Thus, while the genetic origin of *sh4* is not yet clear, its significance as an early-domestication gene distinguishing cultivated *O. sativa* from its wild ancestors is undisputed.

7.2 *Shattering 1 (SH1)*

The *Shattering 1 (SH1)* locus encodes a BEL1-type homeobox transcription factor and the functional mutation, a regulatory SNP located 12 kb upstream of the gene, was shown to decrease expression at the provisional abscission layer, resulting in reduced shattering of varieties that already carry the *sh4* allele (Konishi *et al.* 2006). Unlike the *sh4* mutation that is ubiquitous in *O. sativa*, the *sh1* allele is prevalent only in the *temperate japonica* subpopulation; it is not found in *tropical japonica* nor in *indica* rice accessions. The subpopulation origin of the *sh1* allele was identified using haplotype analysis; *japonica* cultivars carrying

sh1 were found to be more closely related to shattering *O. rufipogon* accessions from northern China that grouped with the *Japonica* varietal group than with shattering wild accessions that clustered with the *Indica* varietal group (Cheng *et al.* 2003, Konishi *et al.* 2006). The nonshattering allele at this locus was thus inferred to have arisen in a *Japonica* or *Japonica*-like ancestor and it became fixed in a restricted portion of the *temperate japonica* gene pool where hard-threshing was desired (Konishi *et al.* 2006). The *sh1* allele differs from the *sh4* allele because of its restricted dispersal among the subpopulations of *O. sativa*. For this reason, it is recognized as a varietal diversification gene and contributes in important ways to our understanding of the *O. sativa* domestication process.

7.3 *Red pericarp (Rc)*

The *red pericarp (Rc)* gene encodes a basic helix–loop–helix transcription factor and the functional version of this gene is required to generate proanthocyanin pigmentation in the rice pericarp, which is characteristic of all wild populations of *Oryza* (Furukawa *et al.* 2006, Sweeney *et al.* 2007). Two different defective alleles at the *Rc* locus have been identified in cultivated varieties and both result in the loss of pigmentation in the pericarp. The *rc* allele differs from the wild-type by a 14 bp deletion in the seventh exon of the gene and the *rc-s* allele contains a SNP in close proximity to the 14 bp deletion (Sweeney *et al.* 2007). Both mutations result in a premature stop that truncates the protein before the bHLH domain and both change the grain color from red to white. Using haplotype analysis and a panel of 440 geographically and genetically diverse germplasm, it was shown that the *rc* allele arose in a *Japonica* or *Japonica*-like ancestor and was responsible for the loss of pigmentation in 98% of white-grained *O. sativa* varieties surveyed, while the *rc-s* allele arose in an *aus* or *aus*-like ancestor (*Indica* varietal group) and accounted for the remaining 2% of white-grained *O. sativa* varieties in the study (Sweeney *et al.* 2007).

White pericarp provides an example of a trait that clearly differentiates cultivated from wild rice. While pericarp color is not considered to be essential to the domestication process, it is genetically and biochemically related to some aspects of seed dormancy, a critical domestication trait (Sweeney *et al.* 2007). Under human selection, the *rc* allele became widely disseminated in all five populations of *O. sativa*, while the *Rc-s* allele remained largely restricted to the *aus* subpopulation. The two independent origins and different evolutionary trajectories of these alleles offer a fascinating opportunity to trace the diversity of human interactions and cultural exchanges in Asia.

7.4 *Grain size 3 (GS3)*

The complex inheritance of grain size in rice is being unraveled through the recent cloning and characterization of several genes affecting the size and shape of the rice grain. *Grain size 3 (GS3)* is located in the pericentromeric region of

chromosome 3 and encodes a novel protein that contains several conserved domains including a phosphatidylethanolamine-binding protein (PEBP)-like domain, a transmembrane region, a putative tumor necrosis factor receptor/nerve growth factor receptor (TNFR/NGFR) family domain, and a von Willebrand factor type C (VWFC) domain (Fan *et al.* 2006). Comparative sequencing analysis identified a nonsense SNP in the second exon of the gene that causes truncation of the C-terminus of the protein, resulting in the recessive (long-grain) phenotype. Transformation with the wild-type allele (short-grain) was shown to complement the long-grain phenotype, confirming that *GS3* acts as a negative regulator of seed size in rice (Takano-Kai *et al.* 2009).

The *GS3* locus had been identified as a major QTL for grain mass and grain length in at least ten previous studies using a variety of both intraspecific and interspecific populations, suggesting this gene was an important factor during the evolution of modern rice varieties. To investigate the evolutionary origin of the functional mutation, haplotype analysis was performed across the *GS3* genomic region in a diverse panel of *O. sativa* germplasm (Takano-Kai *et al.* 2009). This analysis demonstrated that the functional SNP occurred in a *Japonica* genetic background, with all long-grained *Indica* cultivars possessing a *Japonica* genomic region containing the functional SNP at *GS3*. This study presents an intriguing evolutionary puzzle, whereby an allele contributing to the long-grain trait associated with the *Indica* varietal group was shown to have originated in *Japonica*, which is traditionally thought of as possessing short to medium grains.

7.5 Grain incomplete filling 1 (*GIF1*)

The *Grain incomplete filling 1 (GIF1)* gene was recently shown to encode a cell-wall invertase that regulates sugar levels in specific tissues of the developing grain, as well as in elongating internodes and roots where sugars are required to support cell division and growth (Wang *et al.* 2008). By regulating the unloading of sucrose in the ovular and stilar vascular tissues of developing grains, *GIF1* was shown to be a key regulator of starch synthesis in the endosperm during grain filling. The gene was originally identified in a mutant population because it had grain-filling defects, but natural variation was subsequently identified in the promoter region that distinguished wild and domesticated rice. The wild *GIF1* allele was semi-dominant over the domesticated allele, and gene expression was detected in multiple tissues of developing seeds (vascular trace tissue, pericarp, and endosperm) in *O. rufipogon*, while in *O. sativa*, *GIF1* expression was constrained to the ovular vascular trace tissue. Expression patterns were similar in *Indica* and *Japonica* rice, and the restricted expression pattern in the cultivars contributed to enhanced grain weight, and ultimately grain yield.

The *GIF1* promoter region had a significant Tajima *D* statistic in a panel of *O. sativa Indica* (13 Chinese and 1 American accession) and *Japonica* (16 Chinese, 5 Japanese, and 1 French accession) compared with a set of random gene fragments from elsewhere in the genome, and there was a reduction in silent site diversity (π)

in *O. sativa* compared with *O. rufipogon* (Wang *et al.* 2008). Together, these data provided evidence that the *GIF1* promoter was a target of artificial selection in both *Indica* and *Japonica* rice during domestication. While the panel of germplasm used in this study was largely restricted to *Indica* and *Japonica* germplasm accessions found in China, it is noteworthy that the allele was common to both major varietal groups. What is not yet clear is whether this allele is widely disseminated in genetically and geographically diverse landrace accessions of *O. sativa* that originated outside of China.

7.6 *Seed width 5 (SW5)*

The *seed width 5 (SW5)* gene encodes a product of unknown function that is responsible for increased grain width, due to an increase in the rows of specialized cells with rigidified walls in the epidermis, especially the outer glume (lemma), of the rice flower (Shomura *et al.* 2008). A 1,212 bp deletion was diagnosed as the functional nucleotide polymorphism leading to thicker, heavier grains in the *temperate japonica* variety Nipponbare, compared with the *aus* variety Kasalath. The identity of the gene was confirmed by a complementation test in which the dominant, Kasalath allele was used to transform Nipponbare, leading to reduced grain width, and an experiment whereby the seed mass of Kasalath was reduced by transformation with an RNAi construct for the *SW5* gene. In addition, an association analysis was performed based on analysis of over 100 landrace varieties, including both *Indica* and *Japonica*. The deletion in the Nipponbare allele of *SW5* was clearly associated with an increase in rice grain width (Shomura *et al.* 2008).

The association analysis was also used to investigate the distribution of the *sw5* allele in this diverse panel of landraces, and only lines from the *Japonica* varietal group were found to carry the *sw5* allele (Shomura *et al.* 2008). This led to the conclusion that the *Indica* domestication process was distinct from that of *Japonica*, despite the fact that the two subgroups shared other domestication alleles. Further, when landraces were analyzed for combinations of domestication alleles, it was found that many *temperate* and *tropical japonica* cultivars carried *sw5*, but only a subset of *temperate japonica* cultivars carried *sh1*, and whenever *sh1* was present, so was *sw5*. This suggested that *sh1* was a relatively recent mutation and that it may have originated in a landrace that already carried the *sw5* allele (Shomura *et al.* 2008). Together, these alleles contribute to the diversification of *temperate japonica* rice and help differentiate its grain characteristics from those of the other subpopulations of *O. sativa*.

7.7 *Prostrate growth 1 (PROG1)*

The *Prostrate growth 1 (PROG1)* gene encodes a putative Cys₂-His₂ zinc-finger protein that is localized in the nucleus and expressed in unelongated basal internodes (axillary meristems where tiller buds are produced). It acts as a transcription factor and

regulates the transition from prostrate to erect growth habit (Jin *et al.* 2008, Tan *et al.* 2008). This was an important evolutionary step defining plant architecture and was widely selected for during domestication, though many wild populations are erect and some cultivars (i.e., deep-water varieties) retain the prostrate habit. Equally important to the process of domestication is the fact that variation in the *PROG1* locus also affects tiller number and the number of primary and secondary branches on the panicle, leading to greater grain number and higher grain yield in domesticated rice (Tan *et al.* 2008). Site-directed mutagenesis experiments identified a single nucleotide polymorphism in the coding region of *PROG1* that was demonstrated to be functionally responsible for the difference between upright and prostrate growth habit (Jin *et al.* 2008). Additional mutations identified in the promoter region were associated with lower mRNA expression levels documented in unelongated basal internodes in erect cultivars compared to prostrate wild accessions. Sequence comparisons between wild and domesticated rice accessions showed that 182 varieties of domesticated rice, including 87 *Indica* and 95 *Japonica* cultivars from 17 different countries, all carried identical mutations in the *PROG1* coding region (Jin *et al.* 2008, Tan *et al.* 2008). These data are similar to those reported for *SH4* (described above) and document that accessions from both of the major varietal groups within *O. sativa* inherited this allele from a single source.

While the *prog1* allele appears to have reached fixation in *O. sativa*, it is interesting to note that there are many diverse wild accessions that also have the upright growth habit, evidence that it is not deleterious in nature. A reasonable interpretation is that this trait may have been a target of natural selection in the wild, where upright growth and greater seed productivity would be advantageous during dry periods, and it was from such upright wild population(s) that *O. sativa* was domesticated. Alternatively, upright wild populations that share an identical *prog1* allele with the cultivars could be feral; haplotype analysis could provide evidence about gene flow from cultivated to wild populations. In any case, *PROG1* appears to have been a target of artificial selection and the upright habit is a defining characteristic of *O. sativa*, suggesting that humans preferred to harvest seed from erect-standing populations.

7.8 *Waxy (Wx)*

The *Waxy* (*Wx*) gene encodes granule-bound starch synthase and is responsible for differences in amylose content of rice grains, a key component of grain quality. There are two functional forms of *Wx*, one that is predominant in both *O. rufipogon* and *indica* varieties (*Wx^a*) and a derived allele that is predominant in *japonica* varieties (*Wx^b*) (Yamanaka *et al.* 2004). The *Wx^b* allele contains a SNP in the 5' splice site of the first intron that causes incomplete post-transcriptional processing and lower amylose production. A second mutation in either *Wx^a* or *Wx^b* creates a recessive *wx* allele that makes rice fully glutinous. Similar to the *Rc* example, independent mutations in either the *Indica*- or the *Japonica*-specific

Wx alleles give rise to virtually identical glutinous phenotypes, but only the Wx^b -derived wx allele became widely disseminated in landrace varieties. Indeed, the *Japonica*-derived wx allele was found in 97% of 353 glutinous samples from both varietal groups collected from diverse regions across Asia (Yamanaka *et al.* 2004).

8 The emerging picture of *O. sativa* domestication

Based on these examples, a pattern emerges whereby a common suite of early domestication alleles are shared by virtually all *Indica* and *Japonica* varieties, while a second type of domestication alleles contribute to the differentiation of the different subpopulations. Most of the widely disseminated domestication alleles analyzed to date appear to have originated in *Japonica* or a *Japonica*-like ancestor and several of these were subsequently introgressed into the *Indica* varietal group (as reviewed by Kovach *et al.* (2007)). Although relatively few domestication genes have been cloned to date, and there is a bias toward analysis of materials originating in China and East Asia, the pattern that is emerging provides the basis for developing a model of rice domestication that can be tested as additional data is generated.

Given the historical and archaeological data, the Yangtze River Valley in China is the most likely geographical location where selection and fixation of some of the earliest domestication-related traits occurred (Normile 1997, Kovach *et al.* 2007, Vaughan *et al.* 2008, Fuller *et al.* 2009). This is consistent with the *Japonica*-like ancestry of *O. rufipogon* populations found in northern China (Wang *et al.* 2008) and with the documented *Japonica* origins of many domestication alleles known today (Kovach *et al.* 2007).

However, there is strong evidence for a protracted and geographically expansive transition from wild to domesticated rice. Under this model, natural selection pressures gave rise to a diversity of ecologically defined *O. rufipogon* populations across Asia, providing the raw material for local cultivation of diverse forms and subsequently for multiple, independent domestications of *O. sativa*. The spread of domestication traits from one gene pool to another provides clear evidence that rice domestication was characterized by episodes of gene flow between localities of cultivation. This process of introgressive hybridization would have been readily achieved (and indeed hard to prevent) via outcrossing between the incipient domesticates and neighboring wild populations of *O. rufipogon* that were ubiquitous across Asia (Lu *et al.* 2002, Song *et al.* 2003) and hybridization would have continually enriched the gene pool(s) of the evolving domesticates (Sang and Ge 2007, Vaughan *et al.* 2008). Given that wild populations were abundantly cultivated prior to the adoption of sedentary agriculture, there would have been numerous opportunities for artificial selection of locally adapted and locally preferred forms carrying introgressions containing valuable domestication alleles.

Genetic and historical evidence suggests that there would have been a virtually uninterrupted, natural bridge of diverse, wild *O. rufipogon* populations that were

geographically and ecologically differentiated throughout the valleys, swamps, savannas, and deepwater environments across a vast swath of geography from eastern China, Vietnam, Laos, Cambodia, Thailand, Myanmar, and across Bangladesh into the Indian subcontinent. These populations could have served as a natural conduit for the highly valued domestication alleles that moved into locally adapted populations as a result of human migration and trade, or as the result of random gene flow, or a combination of both. It is clear that there were numerous opportunities for pre-agricultural people to identify and select favorable traits from locally adapted wild or cultivated populations and that the wild (pre-domesticated) populations could have been carriers for many of the recessive domestication alleles without manifesting the domesticated phenotype (Sweeney *et al.* 2007). This rich and diverse tapestry of genetic variation would have formed a continuum of *O. rufipogon* – *O. sativa* types, providing the backdrop for the slow fixation of a suite of domestication traits that define the domesticated forms of *O. sativa* known today. It would also have opened the door to the stepwise fixation of alleles associated with polygenic traits whereby different local populations were characterized by differing degrees of trait expression (i.e., nonshattering, seed size and shape, etc.).

Available haplotype data strongly suggests that there was a protracted period of gene flow among genetically distinct populations of proto-*Japonica* and proto-*Indica*. This implies both cultural and seed exchange among human populations, due to proximity or possibly due to trade and migration, whereby domestication alleles were gradually introduced into different genetic backgrounds, giving rise to numerous unique combinations of genes that provided the foundation for continued differentiation of the rice subpopulations. Domestication, with its enhanced levels of inbreeding, would have counterbalanced this gene flow and progressively increased the genetic isolation of the *Indica* and *Japonica* gene pools.

The early *O. sativa* landraces were more heterogeneous, had higher rates of outcrossing, and provided a greater continuum of variation than do modern varieties (Sun *et al.* 2002). Nonetheless, molecular evidence points to an ancient divergence between the *Indica* and *Japonica* gene pools (Cheng *et al.* 2003, Ma and Bennetzen 2004, Vitte *et al.* 2004) and genome-wide SNP analysis supports a model of ancient divergence punctuated by episodes of introgression (Ma and Bennetzen 2004, Rakshit *et al.* 2007, Zhao *et al.* 2010). Evidence of correlated selective sweeps in *Indica* and *Japonica* (Gao and Innan 2008) is consistent with the occurrence of shared domestication and grain quality alleles (Yamanaka *et al.* 2004, Li *et al.* 2006, Sweeney *et al.* 2007, Shomura *et al.* 2008, Tan *et al.* 2008, Wang *et al.* 2008, Kovach *et al.* 2009, Takano-Kai *et al.* 2009), but the analysis lacks power to detect the impact of migration. Domesticated forms of *O. sativa* appear to have moved across Asia with humans, peppered with the many varietal diversification alleles that give *O. sativa* its complex identity (Fuller and Sato 2008, Izawa *et al.* 2008).

The documented *Japonica* origin of many key domestication alleles must be juxtaposed onto a gradual and expansive model of introgressive hybridization

whereby locally adapted populations of *Indica*-like and *Japonica*-like ancestors readily accepted the pollen of domesticated relatives, accounting for the dissemination of those alleles across the vast expanse of Asia.

Consistent with this interpretation is the idea that early *Indica* landraces were cultivated for hundreds or thousands of years within the biogeographical range of their tropical wild progenitors with persistent gene flow between cultivated and wild populations. This is in contrast to *Japonica* rice, which was domesticated in a more temperate region, near the periphery of the natural range of its wild progenitor, where it experienced a more intensive domestication bottleneck (Zhu *et al.* 2007, Zhao *et al.* 2010). In this view, the process of varietal differentiation was underway in parts of Asia long before the fixation of shared domestication alleles and the story of rice domestication must be understood as a dynamic interaction between the two processes. One narrative is a tidy story of domestication, but running just beneath the surface is a second narrative that documents a largely uncharted current of diversity, driven by a promiscuous outcrossing habit that continued to enrich the gene pools of *O. sativa*, even as it was slowly reined in by the imposition of inbreeding and the powerful forces of human selection.

9

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14 Domestication of Lima Beans: A New Look at an Old Problem

M.I. Chacón S., J.R. Motta-Aldana, M.L. Serrano S., and D.G. Debouck

Crop domestication has been aptly considered by Jack Harlan (1992) as bringing wild-growing plants into the human household. This deep alteration of ecological relationships between the domestication-candidate and other biota in the novel and very different cultivated ecosystem – the *domus* – was eventually reflected in marked morpho-physiological and, hence, genetic differences between the domesticate and its wild progenitor. These differences, also labeled the domestication syndrome, concern primarily the organs and traits affected by human selection. They are often discrete and continuing, with a few loss-of-function ones (such as the lack of natural seed dispersal mechanisms). The end-point of this continuum (Pickersgill 2007) is full dependence of the domesticate on human activities for growth, reproduction, and long-term conservation.

The origin of domestication has interested scholars because it can be determined with some probability of success, unlike inquiries into the identity of the first farmers and their motivation and purpose for switching from hunting–gathering to agriculture. The question of origin of a crop can be seen from a double perspective: (i) the biological origin, that is, which wild plant gave rise to the crop through cultivation and selection; and (ii) the geographic origin, namely a particular region where this wild plant may have been domesticated. The domestication syndrome may provide clues pointing to the putative wild ancestor, because human selection affects plant part(s) of direct interest to humans, often fruits and seeds. In the case of Lima bean, this wild progenitor still exists, and its domestication syndrome has been discussed already (Smartt 1988, Pickersgill 2007).

1 An ancient and widely distributed crop

Out of eleven bean species in the first edition of *Species Plantarum* Linnaeus (1753) described two that referred potentially to Lima bean: *Phaseolus lunatus* L. for small-seeded materials and *P. inamoenus* L. for large-seeded materials. Linnaeus described these two species on the basis of cultivated materials passed on to him by botanists

and tradesmen, from ‘Benghala’ for the former and from ‘Africa’ for the latter, a sure indication of an ample distribution in the tropical world at that time. Many more species were described in the period 1790 to 1890, that fell under synonymy of these two species (for a full list see van Eseltine 1931), while botanists over the last century (e.g., Piper 1926, van Eseltine 1931, Verdcourt 1970, Westphal 1974) have considered them as a single species. Worth mentioning is the naming of two taxa on the basis of pod and seed size, as if, in spite of the ample diffusion in the tropical world, two morphological entities could nevertheless be singled out.

From historical records, Lima bean has been reported in natural conditions in the Americas as far north as North Carolina and Delaware (Carter 1949, Baudoin 1989) and central California (Kaplan and Kaplan 1992), and as far south as the Arica region of Chile (Bird and Rivera 1988) and Misiones in Argentina (Burkart 1943). In Africa, it has been introduced in many regions, from Nigeria (Baudoin 1989) to Ethiopia (Westphal 1974) and southwards to the Cape region and Madagascar (Baudoin 1989). In Asia, it is known from Burma, Java, and the Philippines (Safford 1917).

2 Linguistic evidence

The following observations can be made from a compilation of vernacular names given by different agricultural groups of the Americas (Table 14.1). First, there are many names that differ from the Spanish ‘*frijol lima*’ or ‘*haba de Lima*’ (equivalent to Lima bean). The names do not seem to be related but originate in many Amerindian languages that are not closely related (Cavalli-Sforza *et al.* 1994). They are possibly old and continue to be used until today even if these local communities speak Spanish. A language may need some 6,000 years to fully develop and separate from another one (Dixon 1997, Nichols 1998). Some words are widespread, such as ‘ib’ in the peninsula of Yucatan and ‘pallar’ on the coast of Peru, reflecting perhaps their longest and largest strongholds in traditional Latin America. The word used in Haïti in the Caribbean, ‘*pois souche*’, lacks specificity because ‘*pois*’ (= pea) may eventually refer to any grain legume, but farmers have, however, noticed the rootstock (‘*souche*’ = stump) as a clear reference to the pluriannual habit of Lima bean.

3 Archaeological evidence

There are few archaeobotanical records and, when available, not all dates have been verified by Accelerator Mass Spectrometry (Table 14.2). Further, the presence of macro-remains such as pods and seeds depends very much on appropriate conditions for conservation, which bias their ecological distribution towards dry areas. Keeping in mind this situation, the records for the Andes are much older than the remains in Mesoamerica. In spite of this, no seed of Andean Lima bean

Table 14.1. Vernacular names given to the Lima bean in the Americas, places where registered, and possible language involved

North of Panama and the Caribbean			South of Panama		
<i>comba</i>	Guerrero		<i>tapiramo</i>	Guárico	
<i>pecta</i>	Guerrero		<i>tabla</i>	Cundinamarca	
<i>shiumin</i>	Veracruz	Totonaco	<i>cacha</i>	Valle	Paez
<i>ishuet</i>	Chiapas		<i>calentano</i>	Cauca	
<i>patashete</i>	Chiapas		<i>torta</i>	Nariño	
<i>xvet</i>	Chiapas	Tzotzil	<i>torta</i>	Imbabura	
<i>ib, ibes</i>	Campeche	Maya	<i>layo</i>	Cajamarca	
<i>ib, ibes</i>	Yucatán	Maya	<i>pallar</i>	Lambayeque	Quechua
<i>chilipuca</i>	El Salvador		<i>pallar</i>	La Libertad	Quechua
<i>ixpanqué</i>	Suchitepéquez	Kiche	<i>pallar</i>	Ica	Quechua
<i>furuna</i>	Japala	Pocomam	<i>palatu</i>	Cochabamba	
<i>pois souche</i>	Haïti	Créole	<i>chorca</i>	Chuquisaca	

Sources: McBryde 1947, Patiño 1964, Martínez 1979, Breedlove and Laughlin 1993, Cavalli-Sforza *et al.* 1994, Herlihy 1997.

Table 14.2. Archaeological records for Lima bean in the Americas: sites and years before present
NC, noncalibrated date; pC, pre-Ceramic.

North of Panama		South of Panama	
Río Zape, Durango, Mexico	570	Huacaloma, Cajamarca, Peru	2,400
Dzibichaltún, Yucatan, Mexico	1,300	Guitarrero, Ancash, Peru	3,500 (pC)
Tehuacán, Puebla, Mexico	500	Chilca, Lima, Peru	5,600 (pC)
Ocampo, Tamaulipas, Mexico	500 (NC)	Arica, I Region, Chile	2,000 (NC)
Verde Valley, Arizona, USA	700 (NC)		

Sources: Kaplan and MacNeish 1960, Kaplan 1965, Bird and Rivera 1988, Piperno and Pearsall 1998, Kaplan and Lynch 1999.

types has ever been found in archaeological sites in Mesoamerica, nor has Mesoamerican germplasm been identified on the Peruvian coast (Kaplan 1971). The oldest records for Peru are at the Guitarrero Cave and Chilca and both are pre-Ceramic (Kaplan and Lynch 1999). One can, therefore, question their type of use in the absence of pottery to cook them. No transition from wild to domesticated seed types has been observed; instead, only fully domesticated seed types have been recovered. One can assume that domestication would have started much earlier than 5,000 years ago, the age of the oldest remains. A marked increase in seed size indicating a very fast domestication is plausible, but, if so, one wonders about the subsequent stability of seed size for 5,000 years. In addition, if climate has not changed since domestication, the Chilca region is in the middle of one of the driest places on Earth: thus, Lima beans must have been domesticated elsewhere. Additional archaeobotanical or other types of data are necessary to determine where Lima bean was domesticated.

4 A long-standing hypothesis

On the basis of wild Lima beans discovered in the 1930s in Guatemala by Paul Standley, Mackie (1943) proposed an origin of the crop in Guatemala, with three migrations along traditional trade routes and concomitant selections. The ‘Hopi Branch’ included not only materials cultivated in ‘*tierra caliente*’ of Mexico up to the Colorado River watershed, but also materials grown from Florida to Virginia. The ‘Carib Branch’ referred to materials cultivated in Yucatan and across the Caribbean. The ‘Inca Branch’ included materials cultivated in Colombia, Ecuador, and Peru. These three branches, labeled as cultigroups (Baudet 1977, Lioi 1994), may be an oversimplification as the situation in the field seems more complex. The variability in seed morphotypes in areas of traditional cultivation of Lima beans encompasses more than a single cultigroup, even if subsequent introductions of cultivars are possible. This seems to be the case in Cuba (Esquivel *et al.* 1990), Yucatan (Martínez-Castillo *et al.* 2004), and many parts of Peru (Debouck *et al.* 1987).

Additional explorations in Central America and other Neotropical countries have shown that wild Lima beans are present not only in Guatemala – the variety *silvester* of Baudet (1977) – but also in Mexico, where they are distributed from Baja California Sur, the Islas Revillagigedo, and Sinaloa in the northwest, and Tamaulipas, to Puerto Rico to the northeast, and down to Salta and Misiones in Argentina (Freitag and Debouck 2002, Debouck 2008). Furthermore, they are present in all Central American countries, Colombia, and Venezuela. The same small-seeded wild Lima beans could be present in Bolivia and Brazil as well (Debouck 2008).

In light of this wide geographic distribution, other hypotheses about domestication events have been advanced. These include “in the Andes from Peru to central Argentina” (Allard 1960), “east of the Andean highlands” (Kaplan 1965), and “in the interior of South America. . . Amazon Basin. . . origin of large-seeded limas” (Erickson 1982). A more detailed and representative record of the distribution of wild forms of Lima bean was badly needed to make further progress. In 1986, wild Lima beans were found on the western slope of the Andes (Debouck *et al.* 1987). These findings were extended to southwestern Ecuador (Debouck *et al.* 1989a). The discovery of wild forms on the Pacific slope of the Andean range (from the Río Guailabamba basin in Ecuador to the Río Jequetepeque basin in Peru), together with their flower and seed characteristics (Debouck *et al.* 1987), suggested new domestication scenarios.

5 Two gene pools and two domestication events

The utilization of seed storage proteins to trace back origins and domestication patterns in common bean (Gepts *et al.* 1986) incited a similar study on the origin of the different cultigroups of Lima bean from its distinct wild forms. A discriminant variation was found in the lectins rather than in the globulins, as in common

bean, and indicated a similarity of electrophoretic patterns between the small-seeded domesticated Lima beans and a wild form from Jalisco, Mexico, and between the large-seeded domesticated types and a wild form from Cajamarca, Peru (Debouck *et al.* 1989b). These findings were confirmed by additional work on seed storage proteins (Maquet *et al.* 1990, Gutiérrez *et al.* 1995), allozymes (Maquet *et al.* 1997, 1999, Lioi *et al.* 1998), RAPDs on genomic DNA (Nienhuis *et al.* 1995, Fofana *et al.* 1997), RFLPs on ribosomal DNA (Jacob *et al.* 1995, Lioi *et al.* 1998), AFLPs on genomic DNA (Caicedo *et al.* 1999), RFLPs on chloroplast DNA (Fofana *et al.* 1999, 2001), and microsatellites on nuclear DNA (Lioi and Galasso 2002).

6 A new look with a different marker

Chloroplast DNA (cpDNA) is usually reported as invariant within a species; thus it is used often in taxonomic studies where different genera are compared (Doyle *et al.* 1992). Significant intraspecific variation has, however, been found in wild common bean (Chacón *et al.* 2007), itself with an extensive natural distribution in the Americas (comparable to that of the wild Lima bean). That variation proved to be particularly helpful to identify putative places of domestication events of the common bean (Chacón *et al.* 2005). The internal transcribed spacers of ribosomal DNA (ITS/5.8S) have also proven to be useful for intraspecific studies in plant populations (Dick *et al.* 2003, Saslis-Lagoudakis *et al.* 2008). In the present research, DNA sequencing on two cpDNA intergenic spacers (*trnL-trnF* and *atpB-rbcL*) and the ITS/5.8S region was performed to investigate genetic relationships among wild and domesticated Lima beans (Motta-Aldana *et al.* 2010). The Neighbor-Joining (Saitou and Nei 1987) topologies built on the basis of cpDNA and ITS/5.8S polymorphisms reveal three gene pools: one gene pool called “AI” with wild forms from southwest Ecuador and northwest Peru and large-seeded cultivated forms from the same region. A second gene pool called “MII” includes mostly wild forms from Mexico east of the Tehuantepec isthmus, different countries of Central America, Cuba, Colombia, eastern Peru, and Argentina, and two small-seeded domesticated accessions from Brazil. A third gene pool called “MI” includes mostly wild forms from Mexico west of the Tehuantepec and small-seeded domesticated forms from the same region and from Central America and South America. From the coefficients of differentiation among populations (Table 14.3, see Serrano-Serrano *et al.* 2010 for additional information), the three gene pools identified among wild forms seem equally distant, which suggests they diversified very early in the history of the species.

This result involving the “Mesoamerican” wild Lima bean (= *P. lunatus* L. var. *silvester* Baudet) was unexpected. Although found initially in Central America and the Caribbean, it was found later in northern Argentina, and thought to belong to a single ecology, that of lowland subhumid savannas with a marked dry season. This result prompted us to revisit the phylogeny of *P. lunatus*. Its closest relatives,

Table 14.3. AMOVA results and comparisons of differentiation coefficients among the different groups of wild forms of Lima bean

AI (Pacific Range in the Andes), MI (mostly W of Tehuantepec), and MII (east of Tehuantepec, Central America, and rest of South America). Symbols: Φ_{ST} , fixation index for haplotypes; G_{ST} , differentiation on haplotype diversity; N_{ST} , differentiation on nucleotide diversity; **, $p < 0.001$.

Group configuration		cpDNA	ITS/5.8S
AI vs. (MI+MII)			
Source of variation %	Within groups	43.22	48.43
	Among groups	56.78	51.57
Fixation indexes	Φ_{ST}	0.568**	0.516**
	G_{ST}	0.141	0.090
	N_{ST}	0.643	0.549
	Gene flow	Nm	0.21
AI vs. MI vs. MII			
Source of variation %	Within groups	35.37	29.70
	Among groups	64.63	70.30
Fixation indexes	Φ_{ST}	0.646**	0.73**
	G_{ST}	0.291	0.127
	N_{ST}	0.734	0.745
	Gene flow	Nm	0.09
MI vs. MII			
Source of variation %	Within groups	40.39	23.72
	Among groups	59.61	76.28
Fixation indexes	Φ_{ST}	0.596**	0.763**
	G_{ST}	0.199	0.062
	N_{ST}	0.654	0.701
	Gene flow	Nm	0.11

P. augusti Harms and *P. pachyrrhizoides* Harms, are distributed today in the Andes, from Ecuador down to Argentina, and they have been shown to be closely related to the Andean form of wild Lima bean (Caicedo *et al.* 1999) (here the “AI” gene pool). The tertiary gene pool of *P. lunatus* involving other species of *Phaseolus* section *Paniculati* is distributed today in Mexico and eastern and southeastern United States (Freytag and Debouck 2002). A consensus tree based on ITS/5.8S sequences retrieved from GenBank and generated during the present research (Serrano-Serrano *et al.* 2010) shows a group which includes the species of section *Paniculati*, the Andean *Phaseolus* species (*P. augusti* and *P. pachyrrhizoides*), the “AI” gene pool, and then the “MI” and “MII” clusters of *P. lunatus*.

When tentative dating is applied by using the Penalized Likelihood test of Sanderson (2002, 2004), using as constraints minimum and maximum crown node ages as estimated by Lavin *et al.* (2005), one can estimate the separation of the common ancestor to all Lima clusters from the Andean group of species in at least 1.00063 ± 0.08286 million years before present (Mybp) (Serrano-Serrano *et al.* 2010). This is after the closure of the Isthmus of Panama dated at 3.5 to 2.5 Mybp (Graham 1999, Coates *et al.* 2004). The separation of the Andean clade “AI” from

the two Mesoamerican clades “MI” and “MII” would have occurred at 1.1 Mybp. So the formation of *P. lunatus* as a species in the Andean region, itself in active uplift (Taylor 1995), is a plausible scenario; separating from its sister species that would become its secondary gene pool, it migrates back to Central America and Mexico. Soon after their formation, the three clades were isolated geographically or ecologically; “AI” itself became restricted to the western Andes of Ecuador and northern Peru where it survives today. One should note that wild *P. lunatus* is not the only species with migrations across the three major geological gaps of Central America (i.e., the Isthmus of Tehuantepec, Lake Nicaragua, and the Isthmus of Panama), with consequences for the distribution of its genetic diversity. Such migrations have been mentioned for wild common bean (Chacón *et al.* 2007) and the genera *Manihot* (Chacón *et al.* 2008), *Platymiscium* (Saslis-Lagoudakis *et al.* 2008), and *Lupinus* (Hughes and Eastwood 2006).

The possibility of two independent domestications seems beyond doubt, as they are supported equally by both cpDNA haplotypes and ITS/5.8S information (Figure 14.1). One domestication took place within the range of the wild form present in southwest Ecuador and northwest Peru, and gave rise to the large-seeded cultivars (the so-called “Big Limas”). These were further distributed in the Andes, e.g., to the northeast in Cundinamarca (Colombia) and to the southeast in Chuquisaca (Bolivia), as an indication of their early diffusion. Another domestication took place west of the Isthmus of Tehuantepec, and gave rise to many small-seeded domesticated varieties of Mexico, Central America, the Caribbean part of Colombia, the states of Mato Grosso and Espírito Santo of Brazil, and the province of Formosa of Argentina. The marker itself and the uneven sampling of the wild forms in western Mexico do not allow designation of a more specific location for now. Surprisingly, there are two cultivated varieties (from the states of Minas Gerais and Ceará in Brazil) sharing the haplotypes of group “MII”, opening up the possibility of a third domestication event, but with little evidence for a specific geographic location for the putative event.

On the basis of nucleotide diversity, a reduction of genetic diversity occurred during both domestication events (Table 14.4). This founder effect is equally severe for both domestications.

7

Conclusions

Lima bean is, with maize, cassava, arrowroot, and squash (Smith 1997, Dickau *et al.* 2007), among the first crops domesticated in the Americas, and the crop with the widest diffusion in post-Columbian times. The resulting duration of the period under domestication and the pantropical distribution led, under human selections in different ecologies, to the formation of thousands of landraces that are often difficult to classify or trace back to their respective domestication centers (thus, the numerous names given in the past by botanists and the variation noted about geographic origins).



Figure 14.1. Mesoamerican and Andean domestication centers proposed for Lima beans on the bases of (a) chloroplast and (b) ITS/5.8S polymorphisms.

The section of the genus – *Paniculati* – to which *P. lunatus* belongs, was differentiated possibly during the Pliocene of the Tertiary era when Central America was not yet connected to South America and is found in areas of very active geological formation. A branch of the *Paniculati* – the future secondary gene pool of the Lima bean – migrated to northwest South America once the Isthmus of Panama was completely closed (3.5 to 2.5 Mybp) and differentiated into *P. augusti*, *P. lunatus*, and *P. pachyrrhizoides*.

Although wild forms are badly needed from some countries (e.g., Brazil, Bolivia, Paraguay, Panama, and Venezuela) to obtain a better picture, current data suggest that three gene pools exist in wild *P. lunatus*. One gene pool, AI, is today restricted to the Pacific slope of the Ecuadorian and north Peruvian Andes, but seems to be a relic of the Andean origin of the species. Two gene pools, MI and



Figure 14.1. (*cont.*)

MII, were later formed and separated with migrations towards the tropical lowlands of western Mexico (MI) and the rest of Central America and South America (MII).

When humans entered the Neotropics at least some 15,000 years ago (Dillehay 2000), they found wild Lima beans to be widespread, yet they domesticated this species in just two or three locations. The reduced number of domestications may be due to the presence of the highly toxic compound linamarin in all plant parts, including the seed. However, other explanations cannot be excluded because other species, including species of *Phaseolus*, also underwent only a few domestications, in spite of the absence of linamarin. One domestication of *P. lunatus* took place within the range of the AI gene pool, with further diffusion towards the coasts of Peru and Chile and inter-Andean valleys towards the Cundinamarca department of Colombia and the Salta province of Argentina. This domestication took place

Table 14.4. Nucleotide diversity and founder effect in gene pools AI and MIN, number of studied accessions; π , nucleotide diversity; SD, standard deviation.

Domestication event	Population	N	$\pi \pm SD$	Founder effect (%)
cpDNA				
Andean (AI)	Wild	10	0.00140 $\pm$ 0.00066	
	Domesticated	15	0.00011 $\pm$ 0.00010	92.1
Mesoamerican (MI)	Wild	18	0.00108 $\pm$ 0.00027	
	Domesticated	29	0.00000 $\pm$ 0.00000	100
Average founder effect for cpDNA				96.1
ITS				
Andean (AI)	Wild	10	0.00692 $\pm$ 0.00137	
	Domesticated	14	0.00287 $\pm$ 0.00109	58.5
Mesoamerican (MI)	Wild	7	0.00275 $\pm$ 0.00103	
	Domesticated	31	0.00144 $\pm$ 0.00048	47.6
Average founder effect for ITS				53.1

at least 5,000 years ago, in a pre-ceramic context and in an area where, although wild common bean is present (Debouck *et al.* 1993), common bean was not domesticated (Chacón *et al.* 2005). There was thus no domestication blueprint to follow in the central Andes, perhaps in contrast with the Mesoamerican situation.

Another domestication from the MI gene pool took place, tentatively located in western Mexico, perhaps in an area where Lima bean is no longer important as a food crop. A third domestication in the MII gene pool is possible, but incomplete sampling of the wild form in Brazil does not yet allow us to reach a firmer conclusion. Additional explorations, rather than studying existing collections with another marker, is key to a better understanding of patterns of genetic diversity of this crop. These explorations will help secure what seems to be the largest reservoir of genetic diversity – the wild forms – in this species, given the importance of the founder effect, also observed here, as it has been in other Neotropical crops (e.g., maize: Matsuoka *et al.* 2002; cassava: Olsen and Schaal 1999; potato: Spooner *et al.* 2005).

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15 Genetic Characterization of Cassava (*Manihot esculenta* Crantz) and Yam (*Dioscorea trifida* L.) Landraces in Swidden Agriculture Systems in Brazil

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Swidden or slash and burn agriculture begins in prehistory and has been modified by humans with the addition of various components through its evolution (Martins 2001). In pre-Columbian times, only some indigenous people of the Americas became involved in agriculture. In North America, the Atlantic tribes reached this stage. All the Central American tribes cultivated the soil, whereas in South America the traditional swidden field is an inheritance from the Indians, who used fire to burn the woods and subsequently prepare fields for cultivation for three consecutive years (Oliveira *et al.* 1994). As productivity declines owing to depletion of soil nutrients, the area is abandoned, leading the way for ecological succession. Once abandoned, fields are allowed to return to a more natural state as native plant and tree species reclaim the field. As a result, over a period of time soil nutrient levels can return to pre-disturbance levels, although the resulting ecosystems often retain a preponderance of plant species used by humans. While recovering, abandoned fields (also known as “swiddens”) are typically used by humans as a source of fruits, nuts, fibers, medicinal plants, and game. Once ecosystem recovery is sufficiently advanced, the field may be used again for cultivation (Cornell and Miller 2007). This agriculture model, which uses low energy input and intense family labor, is practiced in different regions of the world, such as the cultivation of rice fields in Asia and the itinerant cropping systems in Africa (Martins 2001, Altieri 2002).

In Brazilian swidden agriculture, the generation and amplification of crop species diversity by farmers has caught the attention of many researchers, as it is related to a complex system of shifting cultivation, manipulation of wild species by transplanting, harvesting of wild species, attraction of game by increasing the density of fruit trees, and a particular spatial arrangement of the plants in the

fields. This allows inter- and intraspecific hybridization to occur, which is a key mechanism for the amplification of genetic variability (Martins 1994, 2001). Therefore, the traditional communities are responsible for the maintenance and increase in species biodiversity cultivated and managed by these farmers (Hanazaki *et al.* 1996). Traditional swidden fields are destined towards subsistence food production, where associated cropping is a constant practice.

Swidden fields appear to be chaotic systems, where everything is planted without a pre-established order, reproducing forest diversity at a reduced scale (Oliveira *et al.* 1994). Species cultivated in traditional agriculture can be considered permanent suppliers of new genetic materials, considering that evolutionary processes are constantly active in these populations (Brush 1995). In addition, these farmers possess a great amount of knowledge about the management peculiarities of the diversity they maintain, providing a continuity of evolutionary processes involved in the relationship between humans and the cultivated or managed crop plants. However, the risk of loss of this genetic diversity is high nowadays. Peroni and Hanazaki (2002), conducting a survey of the current and lost diversity of cultivated varieties of many crop species in the coastal areas of the Atlantic Forest, concluded that part of this loss is due to the abandonment of the swidden fields by the farmers' sons. Hence there is a necessity for strategies and conservation politics within the traditional communities situated in these areas. When the role of the traditional human populations, maintainers of genetic diversification, is interrupted, either by land conflicts, by forced migration, or problems of a different nature, the generation of new varieties no longer exists (Martins 2001). In the past few years, the abandonment of agriculture activity has caused, in the scientific community, a concern about the strategies to be utilized for the maintenance of *in situ* genetic diversity, preserved by the traditional agriculturists and indigenous populations in Brazil.

Several studies have tried to reveal the strategies used by the traditional farmers in maintaining a high genetic diversity of crop plants, with emphasis on the vegetatively propagated species in the lowlands of South America such as cassava (*Manihot esculenta* Crantz), sweet potato (*Ipomoea batatas* (L.) Lam.), tannia or cocoyam (*Xanthosoma sagittifolium* L. Schott.), arrowroot (*Marantha arundinacea* L.), marble treebine (*Cissus gongylodes* (Baker) Burch. ex Planch.), groundnut (*Arachis* spp.), and yams (*Dioscorea* spp.). These species were domesticated by indigenous populations, who also developed their cookery based on these products (Cury 1993, Martins 1994, Peroni *et al.* 1999, Faraldo *et al.* 2000, Mühlen *et al.* 2000, Peroni and Martins 2000, Sambatti *et al.* 2001, Peroni and Hanazaki 2002, Silva *et al.* 2003, Elias *et al.* 2004, Bressan 2005, Bressan *et al.* 2005, Peroni *et al.* 2007, Veasey *et al.* 2007, Pereira 2008, Veasey *et al.* 2008, Siqueira *et al.* 2009, 2010). Most of these studies used molecular markers, mainly isozymes (Peroni *et al.* 1999, Faraldo *et al.* 2000, Sambatti *et al.* 2001, Silva *et al.* 2003, Bressan 2005) and microsatellites or simple sequence repeats (SSR) (Mühlen *et al.* 2000, Elias *et al.* 2004, Peroni *et al.* 2007, Pereira 2008, Veasey *et al.* 2008, Siqueira *et al.*

2009, 2010), to characterize the genetic diversity in these crops, maintained by traditional farmers in South and Central America, as well as its distribution among and within swidden fields, communities, and regions.

By using two of these species, cassava and yams, as models, with the addition of two molecular markers (isozymes and SSR), we have studied the genetic diversity and the distribution of this diversity in different levels of organization (swidden field or household, community, municipality, and regions) of landraces maintained and managed by Brazilian traditional farmers.

1 Genetic characterization of cassava in Brazil

Cassava has been the main cultivated plant in Brazilian traditional agriculture and other tropical areas of South America for at least 7,000 years (Allen 1994). This tuber, with numerous vernacular names, is cultivated by several Brazilian traditional households. Studies concerning cassava diversity are still scarce when compared with the great ethnical and territorial diversity of the populations that grow *M. esculenta*. Socio-cultural contexts, as well as economic and ecological processes, exert an influence on the management of this crop with varied intensity. The high diversity observed in the traditional populations that cultivate cassava reflects a pre- and post-colonial history, consisting of migrations, inter-ethnic contacts, and economic pressures (Emperaire *et al.* 2001).

Our aim was to assess the genetic diversity of 42 cassava landraces from selected regions in Brazil using SSR markers and examine how this variability is distributed according to their origin in several municipalities. These plants were collected from homesteads, practicing traditional farming methods, in several municipalities in five regions of Brazil. They were classified into five groups, according to their origin: municipality of Frutal, State of Minas Gerais (MG), municipalities of Eldorado, Cananéia, and Ilha Comprida, in the Vale do Ribeira, State of São Paulo (SP), municipalities of Sonora, Pedro Gomes, Rio Verde de Mato Grosso, Costa Rica, Cassilândia, Paranaíba, and Inocência, State of Mato Grosso do Sul (MS), municipalities of Uarini, Maraã, and Alvarães, in the Mamirauá and Amanã Sustainable Development Reserves, State of Amazonas (AM) and municipality of General Carneiro, State of Mato Grosso (MT) (Figure 15.1).

DNA was extracted according to the methodology described in Siqueira *et al.* (2009). Nine microsatellite loci (GA-5, GA-12, GA-21, GA-126, GA-127, GA-131, GA-134, GA-136, GA-140) were used (Chavarriaga-Aguirre *et al.* 1998) and PCR reactions were performed according to Siqueira *et al.* (2009). Separation of the amplified product was accomplished in polyacrylamide gel electrophoresis and the gels were stained with silver nitrate (Bassam *et al.* 1991). Genetic diversity parameters were estimated using GDA software (Lewis and Zaykin 2001). Allelic frequencies and Nei (1973) genetic diversity parameters were estimated with FSTAT software (Goudet 2001). Cluster analysis was performed with NTSYS software as well as with the Jaccard similarity coefficient and UPGMA

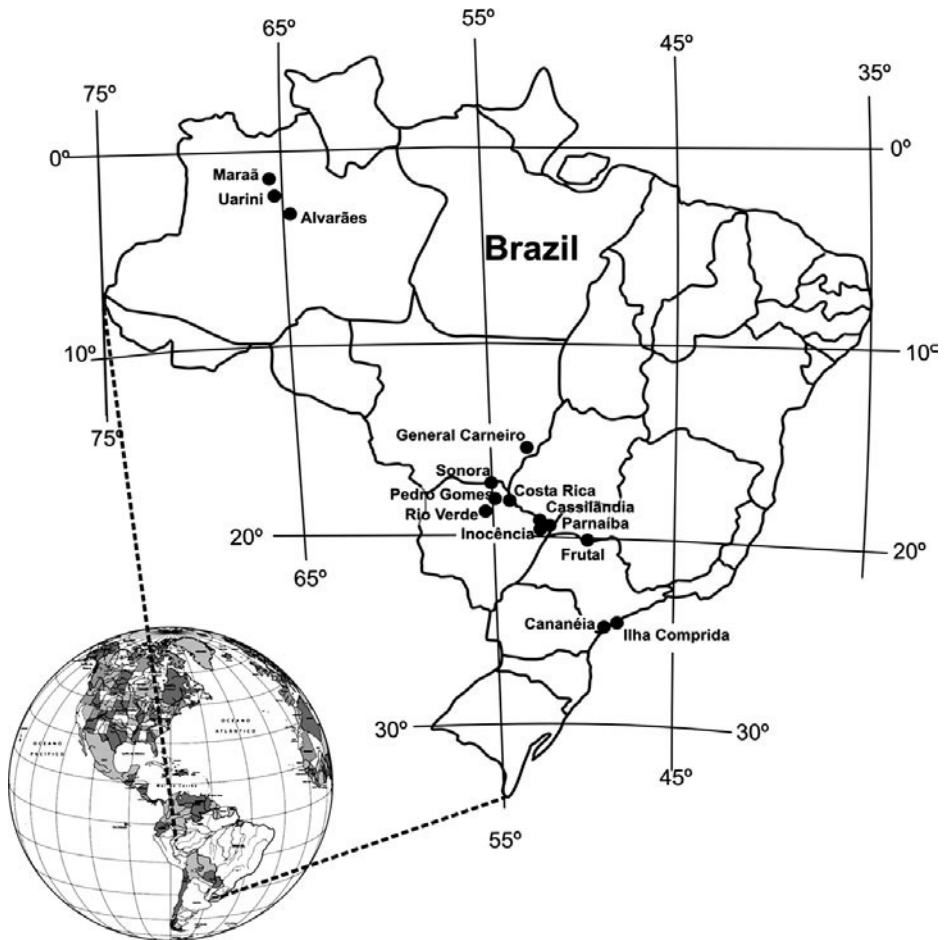


Figure 15.1. Map of Brazil showing the municipalities where the cassava (*Manihot esculenta*) landraces were sampled in this study.

(Unweighted Pair Group Method with an Arithmetic Mean) method as implemented in the NTSYS-pc software (Rohlf 1992).

High genetic diversity was detected in the five regions in Brazil, with an average of 3.3 alleles per polymorphic locus and 96% polymorphic loci (Table 15.1). High gene diversity values of 0.57 on average were also encountered in this study, confirming other studies. For example, gene diversity was found to be high in all the cluster groups of cassava analyzed by Lokko *et al.* (2006), with an average of 0.45. When assessing 283 accessions of cassava landraces from Africa and the Neotropics, Fregene *et al.* (2003) also observed high gene diversity, 0.54 on average with 67 SSR loci. While studying 137 cassava plants from 58 landraces in Brazil, Peroni (2004) obtained an even higher value, 0.64, for gene diversity. All these values are high when compared with the average gene diversity for out-crossing species of 0.21, estimated for all plant species, and 0.16 for dicots

Table 15.1. Number of individuals analyzed (N), mean number of alleles per polymorphic locus ($\bar{A}$), percentage of polymorphic loci (P), mean observed heterozygosity ($\bar{H}_o$), and gene diversity ($\bar{H}_e$) for five groups of cassava

MG, Minas Gerais; SP, São Paulo; MS, Mato Grosso do Sul; AM, Amazon; MT, Mato Grosso.

Group	N	$\bar{A}$	$P(\%)$	$\bar{H}_o$	$\bar{H}_e$
MG	5	2.11	88.88	0.288	0.427
SP	7	3.66	88.88	0.269	0.610
MS	10	3.77	100.00	0.255	0.677
AM	10	3.44	100.00	0.233	0.588
MT	10	3.44	100.00	0.277	0.550
Mean	8.40	3.28	95.55	0.265	0.570

Table 15.2. Nei (1973) genetic diversity parameters for each locus and for the total evaluated loci considering five groups of cassava

MG, Minas Gerais; SP, São Paulo; MS, Mato Grosso do Sul; AM, Amazon; MT, Mato Grosso.

 H_S , within-groups diversity component; H_T , total species-diversity; D_{ST} , between-groups diversity component; G_{ST} , proportion of genetic diversity attributed to the between-groups component, where $G_{ST} = D_{ST}/H_T$.

Locus	H_S	H_T	D_{ST}	G_{ST}
GA-5	0.450	0.453	0.003	0.006
GA-12	0.418	0.618	0.200	0.324
GA-21	0.316	0.574	0.258	0.450
GA-126	0.679	0.711	0.032	0.045
GA-127	0.632	0.737	0.105	0.142
GA-131	0.556	0.610	0.054	0.089
GA-134	0.577	0.616	0.039	0.063
GA-136	0.706	0.730	0.025	0.034
GA-140	0.637	0.668	0.031	0.047
Total	0.552	0.635	0.083	0.131

(Hamrick and Godt 1997). These high values also substantiate both the cassava outcrossing breeding system, with multiloci outcrossing rates estimated at 92% when using isozyme markers (Silva *et al.* 2003), as well as its highly heterozygous nature due to its predominantly vegetative mode of reproduction.

High total diversity ($H_T = 0.64$) was observed in all 42 cassava landraces (Table 15.2), thus confirming the high variability that can be found in this cross-pollinated and vegetatively propagated crop. However, most of this SSR variability was concentrated within ethno-variety groups ($H_S = 0.55$), while lower values were due to the proportion of diversity distributed among the groups themselves ($G_{ST} = 0.13$). Faraldo *et al.* (2000), Mühlen *et al.* (2000), Asante and Offei (2003), Lokko *et al.* (2006), Peroni *et al.* (2007), and Pereira (2008) also observed that most morphological, isoenzymatic, and molecular variability was concentrated within either the cassava “swidden” fields cultivated by traditional farmers or geographic regions. The same pattern was observed with sweet potato landraces

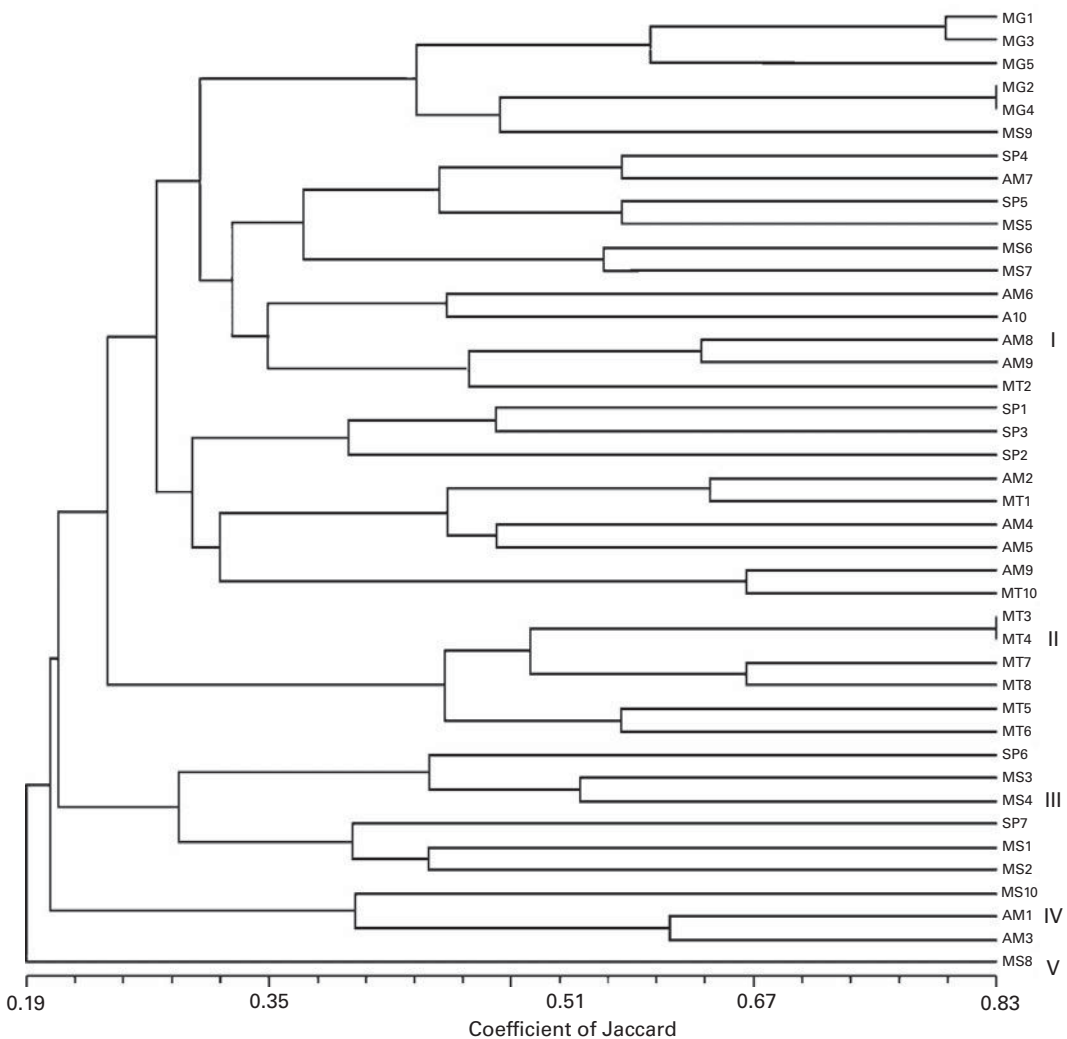


Figure 15.2. Dendrogram obtained with the Jaccard similarity coefficient and UPGMA method, representing genetic relationships among 42 landraces of cassava (*Manihot esculenta*): MG1–MG5 (MG group), SP1–SP7 (SP group), MS1–MS10 (MS group), AM1–AM10 (AM group), and MT1–MT10 (MT group).

from the Vale do Ribeira, with greater genetic variability within swidden fields for both morphological (Veasey *et al.* 2007) and SSR markers (Veasey *et al.* 2008).

In addition to measuring genetic diversity, one of the objectives in our study was to verify how landraces originating from five different regions in Brazil were mutually related. Results showed a greater proximity of landraces from the states of São Paulo, Mato Grosso do Sul, and Amazonas (Figure 15.2). Both Faraldo *et al.* (2000) and Peroni *et al.* (2007) also identified greater genetic similarity among cassava landraces from São Paulo and those from the Amazon. According to these

authors, the samples from São Paulo, represented here by landraces from the Vale do Ribeira, may correspond to a “historical sample” of Amazonian cassava diversity. The Vale do Ribeira is an area with a high diversity of species and varieties, especially cassava, and it is possible that Tupi–Guarani populations were the main disseminators of both cultivation techniques as well as of the species and varieties to be found there (Peroni 2004).

The landraces from Minas Gerais were clustered into a subgroup in the dendrogram (Figure 15.2), within a larger group of landraces from São Paulo, Mato Grosso do Sul, and Amazonas. The origin of these landraces from Minas Gerais, mostly sweet varieties used for home-cooking, is apparently local, with plant material being exchanged among relatives, friends, and neighbors and, according to the villagers, these landraces have been under cultivation in this area over a long period (Angelo and Amorozo 2006).

The landraces from General Carneiro, Mato Grosso were clustered in a separate group (Figure 15.2). In Mato Grosso State, traditional farming is undertaken by local populations, particularly by indians, “quilombolas”, and “pantaneiros”. After the 1950s more recent settlers came from diverse regions of the country, mainly from the south, the northeast, Goiás, and Minas Gerais (Amorozo 2000). General Carneiro is an important area for settlement, the high genetic variability of cassava landraces being a consequence of the introduction of genetic material from the settlers’ places of origin. But certain peculiarities may help to explain the differentiation of local landraces from those of other regions, such as limitations in obtaining new varieties for homestead planting, even of those from the same area, owing to the difficulty and high cost of transportation. Under local conditions, distances as short as 20 km can constitute an isolation factor.

Thus, the migration of human populations is one among the possible reasons for this closer resemblance or greater disparity among plants from the various regions in Brazil and these could be some of the factors contributing to an explanation of the proximity of landraces from São Paulo with those collected in the Cerrado ecosystem of Mato Grosso do Sul and the tropical Amazon Forest.

2 Genetic characterization of yam (*Dioscorea trifida*) in Brazil

Yam belongs to the Dioscoreaceae family, genus *Dioscorea*, which is a very broad genus, found in the tropical, subtropical, and temperate rainy regions (Montaldo 1991). The domestication process of the yam species, which are essentially crops of subsistence agriculture, occurred separately in three continents: Africa (*D. cayenensis* Lam., *D. rotundata* Poir.), Asia (*D. alata* L., *D. esculenta* Burk., *D. bulbifera* L.), and South America (*D. trifida* L.), with intercontinental contacts being relatively recent (Coursey 1976).

Many varieties of yam were introduced into the Americas through the Portuguese and Spaniards in the sixteenth century, during colonization. However, the Portuguese and the Spanish people found the Indians cultivating this plant when

they arrived in America and that is the reason for the name “cara”, a folkname for “caratinga”, “caranambu”, or “acará”, from the Tupi–Guarani language (Abramo 1990). Silva (1971) reports that, at the beginning of the twentieth century, the Rondon Commission found isolated tribes in the extreme northwest of the State of Mato Grosso, in Brazil, cultivating the species *D. trifida*, naming them as “Cará mimoso” (delicate yam), “Cará roxo” (purple yam), “Cará bola” (ball yam), and “Cará rosado” (pink yam). Also known as “cush-cush yam”, *D. trifida* is native to the Guyana region of South America. Because of their relative ease of cultivation and their good flavor they are considered to have a great potential for increased production (Kay 1987).

D. trifida is cultivated by traditional farmers of the Vale do Ribeira in the southern coastal area of São Paulo State. This region presents a peculiarity, i.e., the existence of semi-intact corridors of the endangered Atlantic Forest co-existing with swidden agriculture. This type of agriculture has been practiced for a million years and today it can be considered as an integral part of the ecosystem. Different succession stages occur in the forest, which consists of vegetation mosaics that promote species heterogeneity. These farmers possess an “ecological combining ability”, which promotes the maintenance and generation of genetic diversity of crop plants (Martins 2001), such as *D. trifida*. This type of agriculture survived the various economical cycles that have taken place in the region, because this cultivation model is based on subsistence, in addition to being characterized by a low energy input and intense family labor (Bressan 2005).

In this study, we present data of isozyme and SSR markers to assess the level of genetic diversity in *D. trifida* landraces, cultivated by traditional farmers in the lowlands of South America, including the ‘caiçaras’ from the Vale do Ribeira and Indian and riverine populations from the Amazon.

3 Isozyme marker analysis

Twenty-five *D. trifida* landraces were collected in the municipalities of Cananéia (25°00’S; 47°55’W), Eldorado Paulista (24°31’S; 48°06’W), Iguape (24°42’S; 47°33’W), Ilha Comprida (24°53’S; 47°47’W) and Iporanga (24°34’S; 48°24’W), grown in swidden fields and home gardens by traditional farmers of the Vale do Ribeira. These landraces were assessed with isozyme markers to characterize the genetic diversity and to verify how this diversity was distributed at different hierarchical levels: within swidden fields or home gardens (basic evolutionary unit), between swidden fields and home gardens within communities (cultural units), and between communities.

Six isozyme systems were selected for analysis with polyacrylamide gels: glucose-6-phosphate isomerase (GPI), aspartate aminotransferase (AAT), phosphoglucomutase (PGM), shikimate dehydrogenase (SKD), glucose-6-phosphate dehydrogenase (G₆PDH) and superoxide dismutase (SOD). The system malate dehydrogenase (MDH) was also analyzed using starch gel (Bressan 2005).

Due to the polyploid nature of *D. trifida* (Bousalem *et al.* 2006), complex band patterns were observed in the analyses. Hence, data were assessed as presence or absence of bands. With these binary data, dendrograms were obtained based on the Jaccard similarity coefficient and UPGMA (Unweighted Pair Group Method using Arithmetic means) agglomerative method, using NTSYS-pc (Rohlf 1992). The stability of the clustering in the dendrograms was assessed with 1,000 bootstraps by using the software BOOD version 2.0 and BOOD-P (Coelho 2003). In order to verify the distribution of the genetic variability in the different hierarchical levels, we used molecular variance analysis (AMOVA) with the software Arlequin (Schneider *et al.* 2000). Pearson's correlation coefficient (r) was used to analyze the patterns of spatial variation between Jaccard's dissimilarity indices and the matrix of geographic distances (shortest distance between two households) using NTSYS-pc (Rohlf 1992). Significance of these correlations was tested through Mantel's Z statistic (Mantel 1967), using 1,000 random permutations.

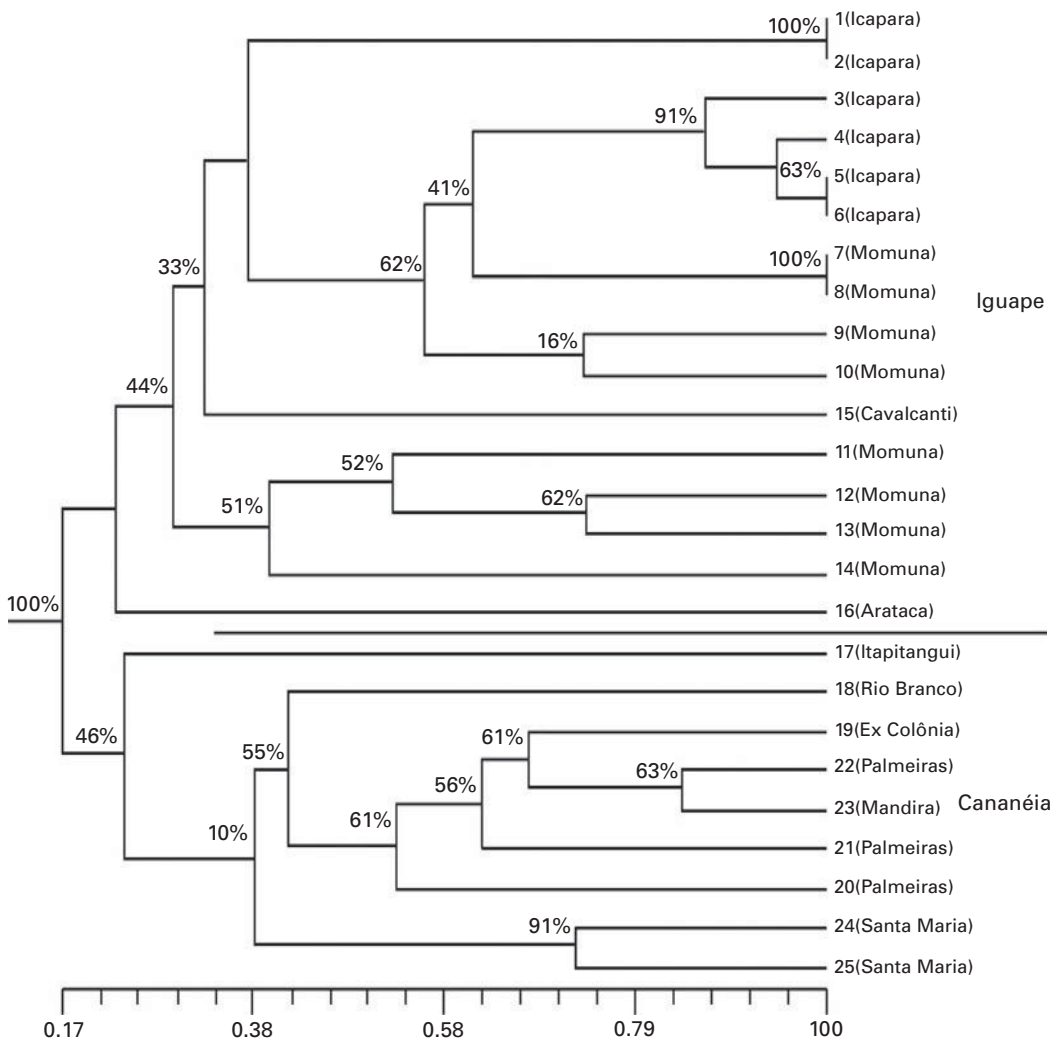
The MDH system showed the highest band number (13) followed by SOD with 12 bands, GOT with 10, SKDH and PGI with 8, G₆PDH with 7, and PGM with 6, for a total of 64 bands. One hundred percent polymorphism was found, that is, no band was present in all the landraces at the same time. The combination of the different isoenzymatic bands allowed the discrimination of 22 of the 25 landraces.

The cluster analysis classified the landraces into two major groups; the first group included the landraces from the Iguape municipality while the second group included those from Cananéia. Therefore, there was a clear separation of the landraces between these two municipalities (Figure 15.3). In three sampled households two accessions represented duplicates (individuals 1 and 2 from household 1, both called "purple yam", individuals 5 and 6 from household 2, both called "white yam", with both households from the Icapara community, and individuals 7 and 8 from household 4, both called "purple yam" by the farmers from Momuna community, all in the Iguape municipality). They showed the same isoenzymatic phenotype within each household, although the farmers have identified them as different materials. The Jaccard similarity coefficient varied from 1.0 to 0.17 (Figure 15.3) indicating a dissimilarity of up to 83%, suggesting a high diversity among *D. trifida* accessions collected in the households of traditional farmers of the Vale do Ribeira. The molecular variance analysis (AMOVA) based on 64 polymorphic bands, showed that 59% of the variability is found between households within communities, 25% between the communities, and 16% within households (Table 15.3).

This is the first report in the literature estimating the isoenzymatic diversity observed among *D. trifida* landraces cultivated by traditional agriculturists from the Vale do Ribeira (Bressan 2005). There are few studies in the literature assessing the genetic diversity of yam species with isozyme markers. Dansi *et al.* (2000), using seven isozymatic systems, identified 227 different genotypes among 467 accessions of the complex *D. cayenensis-rotundata* in Benin. Hamon and Touré (1990) showed a good agreement between morphological and isoenzymatic

Table 15.3. Molecular variance analysis (AMOVA) for 25 landraces of *Dioscorea trifida* from the Vale do Ribeira, São Paulo State

Source of variation	DF	SS	Percentage of total variation
Between communities	9	160.31	24.75
Among households within communities	7	73.95	59.21
Within households	8	14.16	16.04
Total	24	248.44	

**Figure 15.3.** Dendrogram obtained with the UPGMA method and the Jaccard similarity coefficient for 25 landraces of *Dioscorea trifida* using 64 isoenzymatic bands.

polymorphism for 453 accessions of the *D. cayenensis*–*rotundata* complex from West Africa. Lebot *et al.* (1998) studied the genetic relationships among 269 cultivars of *D. alata* originating from the South Pacific, Asia, Africa and the Caribbean with four polymorphic enzyme systems (MDH, PGI, SKDH, G₆PDH). They showed 66 isozyme genotypes but no clear subdivisions could be identified on geographical grounds. Bressan (2005) assessed several landraces from four *Dioscorea* species, *D. trifida*, *D. alata*, *D. cayenensis*, and *D. bulbifera*, maintained by traditional farmers of the Vale do Ribeira with isoenzymatic markers, showing high levels of genetic diversity for all four species.

Pearson's correlation coefficient was null ($r = -0.09$) and nonsignificant, suggesting that there is no correlation between genetic and geographic distances between households and that, probably, the distribution of the landraces is tied to anthropic factors. Veasey *et al.* (2008), when comparing the average Jaccard dissimilarity coefficients for 19 communities with the geographic distances between communities for sweet potato landraces, found a small positive but nonsignificant correlation ($r = 0.147$; $p = 0.054$), indicating that the landraces were also not spatially structured. These results may be attributed to exchange of planting material among the households. Human-induced gene flow would, therefore, intervene in the evolutionary processes of these species.

The great divergence between swidden fields (biological units) within communities (cultural units) is due to the action of evolutionary factors such as genetic drift (genotype losses), natural selection, and anthropic selection acting upon characters of interest. Similar studies with cassava landraces also indicated that for this crop most of the variability is found within swidden fields, as well as within regions (Faraldo *et al.* 2000, Sambatti *et al.* 2001, Peroni and Hanazaki 2002), agreeing with the cross-pollinating mating system of this species (Silva *et al.* 2003).

In our study with yams, which is a dioecious, cross-pollinating species (Zoundjihekpou *et al.* 1997), we found that only one variety was grown in most of the households visited, which explains the lower variability found within households for this species. The results showed, therefore, that most of the *D. trifida* variability was concentrated between households within communities and within municipalities. This high diversity found between households can be explained by the interest of the traditional farmers in maintaining different materials in their communities, whereas each farmer would maintain landraces different from those grown by their neighbors, with the possibility of material exchange. The possibility of new plants arising through seeds, resulting from genetic recombination, is unlikely in the region, as during the collection the farmers did not report seeing flowers or fructification in this species, although a more detailed study in this subject in this area would be recommended. We are left with the possibility of the occurrence of natural mutation, which occurs at low frequency, and other evolutionary forces such as genetic drift, natural selection, and human selection practiced by the agriculturists, to explain the high diversity found between households in the Vale do Ribeira for *D. trifida* landraces.

4 Analysis with microsatellite markers

For genetic analysis with microsatellite markers, eight loci were assessed in 12 *D. trifida* landraces collected in households of traditional farmers in the Vale do Ribeira in two municipalities (Iguape and Cananéia); in the Amazon region in three municipalities (Manacapuru, Itapiranga, and Manaus); and with an Indian tribe called “Myky”, in the State of Mato Grosso.

DNA was extracted from young leaves dried for 24 h at 45°C and then using the protocol based on CTAB extraction buffer (Siqueira *et al.* 2009), modified by using 5% b-mercaptoethanol instead of 1%. The eight primers used in this study (Da1A01, Da1D08, Dab2C05, Dab2D06, Dpr3D06, Dpr3F04, Ym-19, and Ym-28) are described in Tostain *et al.* (2006) and Mignouna *et al.* (2003). The PCR reactions were conducted according to Tostain *et al.* (2006). Bands were visualized in 6% polyacrylamide silver stained gels. Data were assessed as presence/absence of bands, and a cluster analysis was conducted using NTSYS-pc (Rohlf 1992), with Jaccard’s similarity coefficient, and the UPGMA method. The software Arlequin (Schneider *et al.* 2000) was used to determine the distribution of the genetic variability within and between regions through a molecular variance analysis (AMOVA).

The cluster analysis classified the landraces into two groups: the first one included the landraces from the Vale do Ribeira and the landrace cultivated by the Myky Indians in the State of Mato Grosso (Figure 15.4). The second group included the landraces from the Amazon region. The Jaccard similarity coefficient varied from 53% to 95%, indicating the existence of high genetic diversity among the landraces analyzed.

The similarity observed between the landraces grown by traditional farmers in the Vale do Ribeira and the landrace cultivated by the Myky Indians in Mato Grosso may be related to the Indian influence upon the domestication of *D. trifida*, which has been cultivated by the Indians from the coastal areas to the Center-West region in Brazil (Pedralli 1991). Among the Brazilian Indians, the Tupi–Guarani could be mentioned, as they are characterized by being itinerant and highly dispersed along the Brazilian territory, including the State of Mato Grosso and the coastal area of São Paulo State (Ladeira 1992). These Indians used to migrate for long distances carrying along with them samples of the species they traditionally cultivated, among which *D. trifida* is included, typically denominated as “cará” (Schmitz and Gazzaneo 1991). This species has a strong association to these indigenous people who, on the other hand, have a strong influence upon the traditional populations in the Vale do Ribeira region (Bressan 2005). Although the Myky tribe does not belong to the Guarani’s, there may have been contact and even interchange of plant materials with other indigenous people that passed through their territory. However, for a better understanding of this species diversity in the State of Mato Grosso, a higher number of landraces should be sampled in the future.

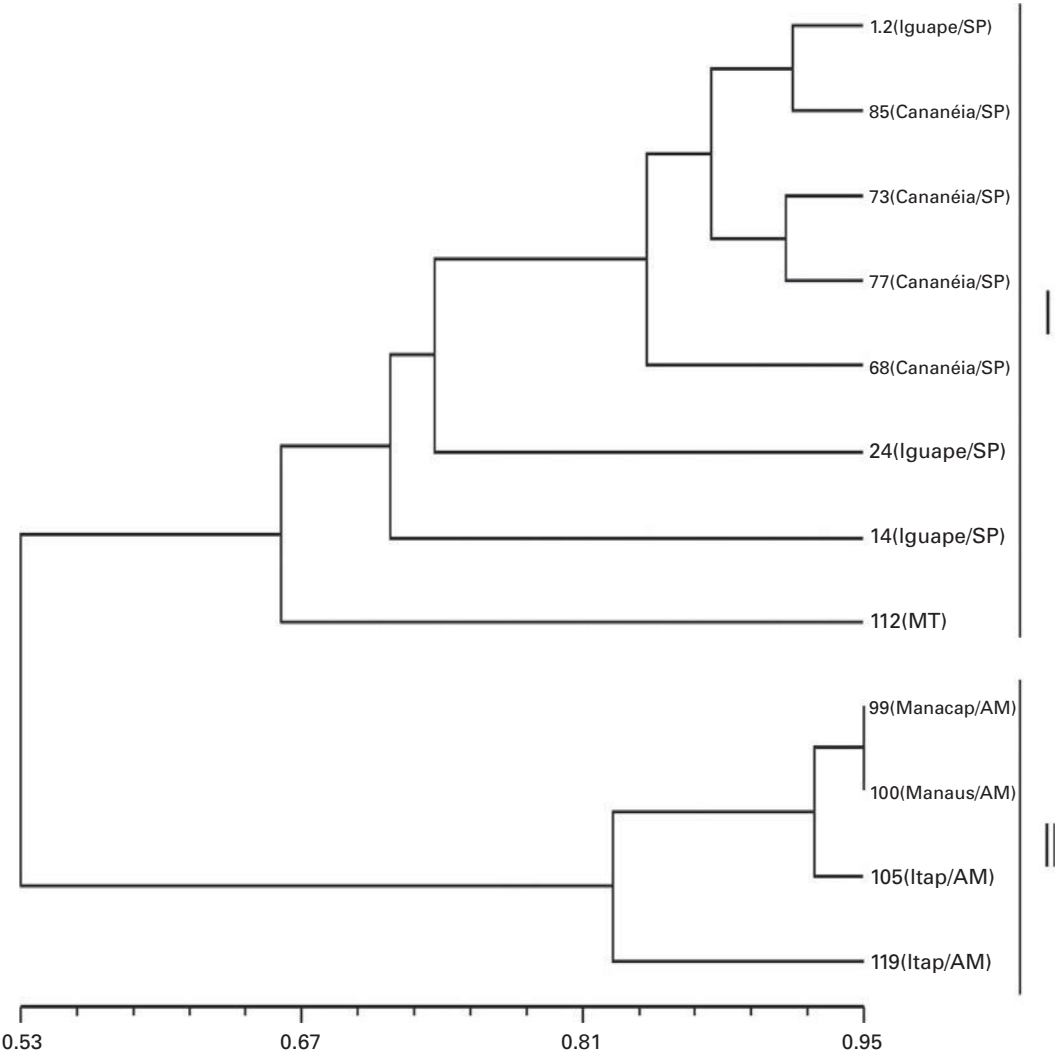


Figure 15.4. Dendrogram obtained with the UPGMA method and the Jaccard similarity coefficient for 12 landraces of *Dioscorea trifida* from the Vale do Ribeira, São Paulo (SP) State (Iguape and Cananéia municipalities), Mato Grosso (MT) State (Myky tribe), and the State of Amazonas (AM) (Manaus, Manacaparu, and Itapiranga municipalities), with eight SSR loci.

The second group, including landraces from three municipalities in the State of Amazonas, showed lower genetic variation, with 82% similarity between landraces (Figure 15.4), which may be related to the smaller sampling ($n = 4$), or to the proximity between municipalities, allowing a greater exchange of plant materials. This fact could be intensified by the practice, common among farmers in the municipalities close to Manaus, of selling their varieties in the main city market, where the exchange of materials could be favored.

Table 15.4. Molecular variance analysis (AMOVA) for microsatellite data of 12 *D. trifida* accessions

Source of variation	DF	SS	Percentage of total variation
Between groups	1	19.083	62.90
Within groups	10	19.000	37.10
Total	11	38.083	—

The molecular variance analysis (AMOVA) showed that 63% of the genetic variability was found between regions (Table 15.4). This result indicates that the long distance between the regions in this study, Vale do Ribeira and Mato Grosso as one group or region, in contrast to the Amazon region, may have contributed for the high diversity between landraces from these regions. This result confirms the separation of the two groups in the dendrogram (Figure 15.4). Within groups, a tendency was observed for the separation of the Cananéia landraces from those of Iguape in the Vale do Ribeira, although this separation between municipalities was more evident with isozyme markers (Figure 15.3). This result is probably occurring because, in contrast to the cassava crop (used for home consumption, as well as for flour and *in natura* commercialization), yam (*D. trifida*) is a crop subjected to human selection based on local interests, where each farmer only maintains the varieties of interest for home consumption. This leads to a lower gene flow between communities in the two municipalities, resulting in materials showing higher diversity between municipalities and regions.

5 Concluding remarks

The molecular marker studies reported here, involving cassava and yam (*D. trifida*) landraces from different regions in Brazil, highlight the important role of traditional farmers in maintaining genetic diversity in these vegetatively propagated crops. These studies showed that the landraces are not strongly structured spatially, which may be due to anthropic factors promoting gene flow among households, communities, and municipalities. The study of *D. trifida* with SSR markers showed a higher diversity between regions, indicating lower gene flow for this species between the Amazon and São Paulo regions, whereas a different result was found with cassava, showing a higher proximity between these two regions. This may be attributable to stronger commercialization in cassava compared with yam.

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16 Pigeonpea: From an Orphan to a Leader in Food Legumes

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More than six billion people of this planet are dependent on nurturing and harnessing agro-ecological biodiversity for food and nutritional security. Human life and civilizations have been influenced not only by cultivated taxa, but also by wild germplasm. The origin and fast-track evolution of agricultural crops aided by domestication have attracted considerable attention from evolutionary biologists, plant explorers, archaeobotanists, geneticists, and plant breeders world-wide in crops such as rice, wheat, and maize. However, legumes (barring soybean) have remained relatively neglected by the researchers.

Globally, pigeonpea is grown on an area of 4.64 million hectares (Mha) annually with production of 3.43 million tonnes, yielding 740 kg ha^{-1} (FAO 2008). In the past three decades India has contributed to more than 70% of global area and production of pigeonpea. India (cultivating 3.53 Mha), Myanmar (570,000 ha), and Nepal (20,988 ha) are the most important Asian countries for pigeonpea production (Table 16.1). In Africa, Kenya (190,000 ha), Malawi (123,000 ha), Uganda (87,000 ha), and Tanzania (67,500 ha) are the leaders.

Pigeonpea is a versatile food legume. Its dried, decorticated split pea (*dhal*) is consumed as protein source in many Asian and African countries. Green seeds and pods are also consumed as a vegetable in parts of India and Africa. The seed husk and pod wall form quality animal feed. The dried stems of pigeonpea are a good source of fuel wood (the calorific value is about half that of coal (Panikkar 1950)), thatch, and material for basket making. Pigeonpea helps in release of soil-bound phosphorus (Ae *et al.* 1990). Like other legumes, pigeonpea fixes about 40 kg ha^{-1} nitrogen per season (Kumar Rao *et al.* 1983). There are also reports of up to 280 kg ha^{-1} of nitrogen fixation (Red de Grupos de Agricultura de Cobertura 2002). Pigeonpea has also been used as a green-manure crop, a cover crop, and food for silkworms (Red de Grupos de Agricultura de Cobertura 2002) and as a host for the lac insect (*Kerria lacca*). The deep root system of pigeonpea breaks the soil hard-pan and helps in nutrient recycling from the deeper layers of soil. Long- and medium-duration pigeonpea varieties have also been successfully used for mountain slope stabilization in southern China and Northern India.

Table 16.1. Global area, production, and productivity of pigeonpea during 2007

Country	Area (ha)	Production (tons)	Productivity (kg ha ⁻¹)
India	3,530,000	2,510,000	711
Myanmar	570,000	540,000	947
Kenya	190,000	105,000	553
Malawi	123,000	89,000	724
Uganda	87,000	79,000	908
Tanzania	67,500	48,500	719
Nepal	20,988	19,245	917
Dominican Republic	17,100	17,100	1,000
Congo	9,500	5,600	589
Haiti	6,200	2,500	403
Panama	5,000	2,100	420
Bolivarian Republic of Venezuela	3,400	3,100	912
Burundi	2,000	1,800	900
Bangladesh	1,600	1,000	625
Jamaica	900	1,000	1,111
Philippines	825	1,350	1,636
Grenada	550	530	964
Trinidad and Tobago	450	1,100	2,444
Comoros	440	320	727
Puerto Rico	285	230	807
Bahamas	200	135	675
Total/mean	4.64 M	3.43 M	739

Source: FAO 2008.

1 Origin and domestication

Following the origin of cultivated pigeonpea [*Cajanus cajan* (L.) Millspaugh; syn. *Cystisus cajan* L., *Cajanus bicolor* DC., *C. flavus* DC., *C. indicus* Spreng., *C. luteus* Bello], possibly from *C. cajanifolius* (Haines) van der Maesen (De 1974, van der Maesen 1980), it has undergone changes typical of the “domestication syndrome” (Harlan and de Wet 1971, Harlan 1975, 1976). These changes are similar to the domestication syndrome of some crops of the families Poaceae (rice, wheat, maize, barley, oats) and Fabaceae (peas, soybean, common bean) (Harlan 1992). The phylogenesis involved changes in the duration of maturity (from perennial to annual to a very short duration), seed dispersal (shattering to nonshattering types), seed dormancy (long dormancy to no dormancy), and harvest index (low to high harvest index). However, pigeonpea has also maintained some wild traits such as its deep root system, indeterminate growth habit, and recovery from stresses.

The primary pigeonpea center of diversity is found on the Indian subcontinent, with a large number of wild species, including the most closely related species *C. cajanifolius* (van der Maesen 1980). A very diverse cultivated gene pool and a few archaeological remains in India strongly suggest that India is the primary

center of origin of pigeonpea. East Africa is regarded as a secondary center of origin. There have been some archaeological references to the presence of pigeonpea seeds in Egyptian tombs of the twelfth dynasty (2200–2400 BC) at Dra Abu Negga (Thebes) (Schweinfurth 1884). However, De (1974) and Vernon Royes (1976) reviewed the origin of pigeonpea and concluded that pigeonpea originated in India. Vavilov (1951) also supported the Indian origin theory of pigeonpea since he found the largest range of diversity of pigeonpea on the Indian subcontinent. The most recent conclusion is that the origin of pigeonpea was in India (van der Maesen 1980).

Pigeonpea belongs to the subtribe Cajaninae, tribe Phaseoleae in the subfamily Papilionoideae, of the family Fabaceae. Pigeonpea is the only cultivated food crop of the Cajaninae subtribe. The other members of the tribe Phaseoleae include many bean species (*Phaseolus*, *Vigna*, *Lablab*, *Macrotyloma*, etc.) consumed by humans. The updated genus *Cajanus* now comprises 32 species, with 18 species distributed in Asia, 15 in Australia, and one in West Africa (van der Maesen 1990). Of these, 13 are endemic to Australia, 8 to the Indian subcontinent and Myanmar, and one to West Africa. The rest of them occur in more than one country. Apart from cultivated pigeonpea, only one wild species, *C. scarabaeoides*, is common and widespread throughout South and Southeast Asia, the Pacific Islands, and northern Australia. The greatest diversity of wild species of *Cajanus* is found in Myanmar, southern China, and northern Australia.

The name pigeonpea originated in Barbados, where the seeds of *Cajanus* were used as pigeon feed. There are at least 350 recorded orthographic variants of the term pigeonpea. In India many ancient Sanskrit names (Adhaki, Adhuku) have modern equivalents as Arhar and Tur. It is also known as Angola pea, Congo pea, Kachang Bali, Ads Sudan, *Cajanus des Indes*, Frijol de árbol, Pois cajan, Puerto Rican pea, Indircher Bohnenstrauch, Lentil du Sudan, Gandul, Gungo pea, Gunga pea, No-eye pea, and Red gram in different parts of the world.

2 Gene pools in pigeonpea

The concept of the gene pool in pigeonpea was laid down by Harlan and de Wet (1971) and has undergone many revisions. Among the members of the Phaseoleae, Cajaninae is well distinguished by the presence of vesicular glands on the leaves, calyx, and pods. Currently, 11 genera are included in Cajaninae, including *Rhynchosia* Lour., *Eriosema* (DC.) G. Don, *Dunbaria* W. & A., and *Flemingia* Roxb. ex Aiton. The members of the earlier genus *Atylosia* closely resemble the genus *Cajanus* in vegetative and reproductive characters. However, they were relegated to two separate genera mainly on the basis of the presence or absence of a seed strophiole. Although the separation of these two genera was questioned by some researchers in the past, it was not taken seriously for want of taxonomic data. The establishment of ICRISAT in 1972 gave a big impetus not only to collect various *Atylosia* species but also for their utilization in the pigeonpea improvement. During the past three decades several researchers both at ICRISAT and in Indian

Table 16.2. Gene pools of pigeonpea

Primary gene pool	Cultivar collections
Secondary gene pool	<i>Cajanus acutifolius</i> , <i>C. albicans</i> , <i>C. cajanifolius</i> , <i>C. lanceolatus</i> , <i>C. latisepalus</i> , <i>C. lineatus</i> , <i>C. reticulatus</i> , <i>C. scarabaeoides</i> var. <i>scarabaeoides</i> , <i>C. sericeus</i> , <i>C. trinervius</i>
Tertiary gene pool	<i>C. goensis</i> , <i>C. heynei</i> , <i>C. kerstingii</i> (?), <i>C. mollis</i> , <i>C. platycarpus</i> , <i>C. rugosus</i> , <i>C. volubilis</i> , other <i>Cajanus</i> spp. (?), other Cajaninae (e.g., <i>Rhynchosia</i> , <i>Dunbaria</i> , <i>Eriosema</i>)

national programs successfully produced fertile hybrids between pigeonpea and *Atylosia*. These studies provided the basis to merge the two genera following international rules of botanical nomenclature. Finally van der Maesen (1986) revised the taxonomy of *Cajanus* and merged the two genera under *Cajanus* following systematic analysis of morphological, cytological, and chemotaxonomical data, which indicated the congenicity of the two genera. Primary (GP 1), secondary (GP 2) and tertiary (GP 3) gene pools have now been identified. These gene pools have been used in transferring agronomically superior traits such as disease resistance, high protein content, tolerance to drought, salinity, cold, waterlogging, and *Helicoverpa*, cytoplasmic-nuclear male sterility (CMS), etc. On the basis of crossability studies done at ICRISAT, different species have been assigned to their respective gene pools (Table 16.2).

Pigeonpea is a diploid species with $2n=2x=22$ somatic chromosomes. There has been no discrepancy in the chromosome numbers of pigeonpea across various reports. Most of the reserchers have found $2n=22$ for the entire genus *Cajanus*. The only exceptions came from *C. kerstingii*, which was reported to have $2n=32$ chromosomes (Lackey 1980; Gill and Husaini 1986). The meiotic behavior and pollen formation are normal in *C. cajan*, and the metaphase I behavior in pollen mother cells was found to be normal by many workers (Kumar *et al.* 1945; Bhattacharjee 1956; Dundas *et al.* 1987), or perfect pairing by Reddy and De (1983). The genome size (IC) of cultivated pigeonpea is reported to be 0.825 (Greilhuber and Obermayer 1998). This genome size corresponds to 808 Mbp.

Pigeonpea in an often cross-pollinated crop with natural outcrossing ranging from less than 1% to 70% (Saxena *et al.* 1990). Outcrossing is largely mediated by insects and to very little extent by wind. Pathak (1970) reported *Apis mellifera* and *A. dorsata* as principal pollinating vectors.

3 Crop improvement

In spite of several useful traits, pigeonpea had remained by and large an “orphan” crop with many wild-type traits. Some of the wild traits in pigeonpea that were



Figure 16.1. A two-year-old pigeonpea tree in Antigua.

addressed by plant breeders were (i) long maturity duration, (ii) excessive plant height and low harvest index, (iii) photoperiod and temperature sensitivity, (iv) susceptibility to *Helicoverpa* and diseases (*Fusarium* wilt, sterility mosaic), and (v) low grain yield. Extensive trait-specific plant breeding research activities were directed towards these issues, with demonstrable progress.

3.1 Early maturity

Cultivated germplasm is of long-maturity duration type (200–300 days). Some perennial landraces may grow like a tree (Figure 16.1) in 2–3 years. Variation in maturity is almost continuous and has been classified into ten maturity groups on the basis of days to 50% flowering (Green *et al.* 1979) (Table 16.3). The long-duration varieties have low seedling vigor, thereby increasing exposure to stresses such as weeds, pests, and diseases. Breeding and selection have enabled development of a range of maturity types (Table 16.3) suitable for different agro-ecosystems and cropping systems.

Extra-short-duration (ESD) lines (Davis *et al.* 1995, Singh 1996) have opened up new cropping niches for pigeonpea. These lines (MN 1, MN 5, and MN 8) flowered in 45–50 days and matured in 70–85 days at ICRISAT, Patancheru (17°N latitude), and have served as an excellent source for earliness in many breeding programs globally.

Table 16.3. Ten maturity groups of pigeonpea

Note: Classification is based on days to 50% flowering at Patancheru (17°N).

Maturity group	Days to 50% flowering	Reference cultivars
0	<60	ICPL 88039
I	61–70	Prabhat
II	71–80	UPAS 120, ICPL 87
III	81–90	Pusa Ageti, T 21
IV	91–100	ICP 6
V	101–120	Maruti, BDN 1
VI	121–130	Asha, C 11
VII	131–140	Hy 3C, ICP 7035
VIII	141–160	Bahar
IX	>160	NDA 1, MAL 13

ESD lines are also grown as a catch-crop (Chauhan *et al.* 1993, Nam *et al.* 1993), and in rice fallows in the short-rainy season in Sri Lanka (Chauhan *et al.* 1999), India, and the Philippines. These lines are used for diversifying cereal-based crop rotations of rice–wheat cropping systems, particularly in the Indo-Gangetic plains. ESD line ICPL 88039 is presently grown on more than 40,000 ha in India and the Philippines, helping preserve the soil fertility and bringing about environmental sustainability to the farming systems.

3.2 Increasing harvest index

Most pigeonpea landraces are tall and grow up to 3 m or more. The harvest index associated with such tall landraces was quite low because of lower grain yield. Such tall lines posed difficulty in taking up plant protection measures such as spraying. Saxena and Sharma (1995) reported 12 types of genetic dwarf in pigeonpea. Dwarfness genes such as *dl* (Saxena *et al.* 1989) served as a source for breeding high-yielding genetically dwarf varieties. The lines bred with this gene were 30%–50% shorter in height and productivity compared with the tall varieties (Saxena 2005). The harvest index of these lines was about 30%–40% higher than that of the tall landraces.

3.3 Reduced photoperiod and temperature sensitivity

The photoperiod and temperature sensitivity of pigeonpea was a constraint to its wider adaptation, and restricted it to the areas between latitudes 35°N and 35°S. Pigeonpea is a quantitative short-day plant, and requires long nights for induction of flowering. The photoperiod sensitivity in pigeonpea germplasm is not only linked to days-to-flowering but also to the amount of biomass produced (Wallis *et al.* 1981). ICRISAT scientists used the Kenya transect, which is near the equator, and selected experimental locations varying from 50 m to over 2,000 m in altitude. In these locations, temperature decreased with higher altitude, thus

providing an “open laboratory”. Results indicated that medium-duration varieties would only flower under short days. Optimum temperature for early flowering and maturity was 22–24°C, indicating that they are suited to medium-altitude environments near the equator. On the other hand, long-duration varieties would flower under short days and low temperature. The optimum temperature for such lines was about 18°C. This material was suited for growing between 900 and 1500 m altitude near the equator and subtropics, where day length is short and temperature is low during autumn/winter (Omanga *et al.* 1995, Silim *et al.* 2006). This strategic research has helped scientists breed varieties for wider adaptability. Now it is possible to grow pigeonpea between latitudes 45°N and 45°S, and it can be cultivated up to 2000 m above mean sea level (msl) in the tropics and subtropics.

3.4 Resistance to pests (*Helicoverpa*) and diseases (*Fusarium* wilt, sterility mosaic)

3.4.1 Resistance to *Helicoverpa*

Losses due to *Helicoverpa armigera* (pod borer) are estimated at US\$310 M annually. A high level of resistance to *Helicoverpa* is not available in cultivated germplasm. Hence, the low-level of resistance is augmented by cultural and biological control means. Significant progress has been made towards transferring resistant genes from the secondary gene pool. Recent results show that while species like *C. albicans* and *C. scarabaeoides* are not preferred for oviposition, antibiosis is present in *C. sericeus*. Attempts are being made to combine these traits together. Some of the recent *C. acutifolius* derivatives registered less than 10% pod borer damage under field conditions.

Genetic transformation has been thought a more viable alternative towards solving this menace. Novel transformation protocols have been optimized for pigeonpea, otherwise considered a recalcitrant crop for obtaining transgenics by using *Agrobacterium tumefaciens*-based binary plasmids carrying *cryIAb*, *cryIIAc*, and soybean trypsin inhibitor (*SBTI*) genes. A large number of putative transformants were generated for the first time and over 50% of them tested positive for the introduced genes. These transformants also showed high gene expression at the transcription level. Soon these will be available for field testing against pod borers (Kumar *et al.* 2004; Sreelatha *et al.* 2005; Sharma *et al.* 2006).

3.4.2 Resistance to wilt

Wilt caused by the soil-borne fungus *Fusarium udum* Butler can cause up to 100% yield loss under epidemic conditions. There are also reports of seed-borne infection under wilting during pod filling stages (Haware and Kannaiyan 1992). Wilt-sick plots have been used for large-scale screening of germplasm lines and breeding materials and a number of resistance sources have been identified at ICRISAT (Reddy *et al.* 1990). Several wilt-resistant varieties (such as Maruti and Asha in India) have been adopted by farmers on a large scale, leading to increased production. Now all advance breeding lines from ICRISAT carry resistance to wilt disease.

3.4.3 Resistance to sterility mosaic

The disease was reported in 1927 but its causal organism remained a mystery. In a relentless effort over decades, ICRISAT and partners were able to identify the elusive causal agent, now named pigeonpea sterility mosaic virus (PPSMV) (Jones *et al.* 2004), which is transmitted by an eriophyid mite (*Aceria cajani*). This breakthrough research, coupled with effective resistance screening, has enabled the breeders to develop several resistant cultivars. ICRISAT has also developed effective and economical diagnostic kits to survey and determine the extent of the disease and the variability of the virus. ICRISAT has been able to deliver these outputs with effective partnerships with researchers in the Indian Council of Agricultural Research, India, and the Scottish Crops Research Institute, UK.

3.5 High yield potential

Until recently the grain yield levels of pigeonpea had remained stagnant between 700 and 800 kg ha⁻¹ for five decades. Crop improvement methods, such as pure-line breeding, population breeding, mutation breeding, and interspecific crosses were used to develop improved varieties. More than 60 pure-line varieties bred in the past have had little or no impact on the productivity of pigeonpea. Therefore, scientists at ICRISAT envisaged breeding hybrids in pigeonpea to overcome the yield barrier. A genetic-male-sterility (GMS)-based hybrid breeding system using partial natural out-crossing (otherwise considered a constraint in varietal seed production) was initiated at ICRISAT (Reddy *et al.* 1978, Saxena *et al.* 1983). The world's first pigeonpea hybrid cultivar, ICPH 8 (Saxena *et al.* 1992) was released in 1992, targeted for diverse agro-ecological conditions, in which it recorded an average 30.5% yield advantage over the best existing variety. In spite of high yields, ICPH 8 could not become popular owing to difficulties in large-scale seed production. This spurred scientists to develop a more efficient cytoplasmic-nuclear male-sterility (CMS) system.

ICRISAT scientists developed CMS lines by combining the cytoplasmic genome of wild relatives with the nuclear genome of cultivated pigeonpea. So far five CMS systems have been developed. A₁ cytoplasm was derived from *C. sericeus*, A₂ cytoplasm from *C. scarabaeoides*, A₃ cytoplasm from *C. volubilis*, A₄ cytoplasm from *C. cajanifolius*, and A₅ cytoplasm from *C. cajan*. A₄ cytoplasm has been most promising, and has offered stable male-sterile lines, excellent frequency of maintainers in the cultivated germplasm, and very high fertility restoration in the F₁ hybrids (Saxena 2008). Using this technology, ICRISAT developed the world's first CMS-based pigeonpea hybrid variety ICPH 2671 (Figure 16.2). The development of the pioneer CMS system and hybrid technology are major milestones in the history of breeding food legumes and hold the promise of breaking the productivity barrier. The CMS has now been introgressed into agronomically superior varieties for developing locally adapted hybrid varieties.

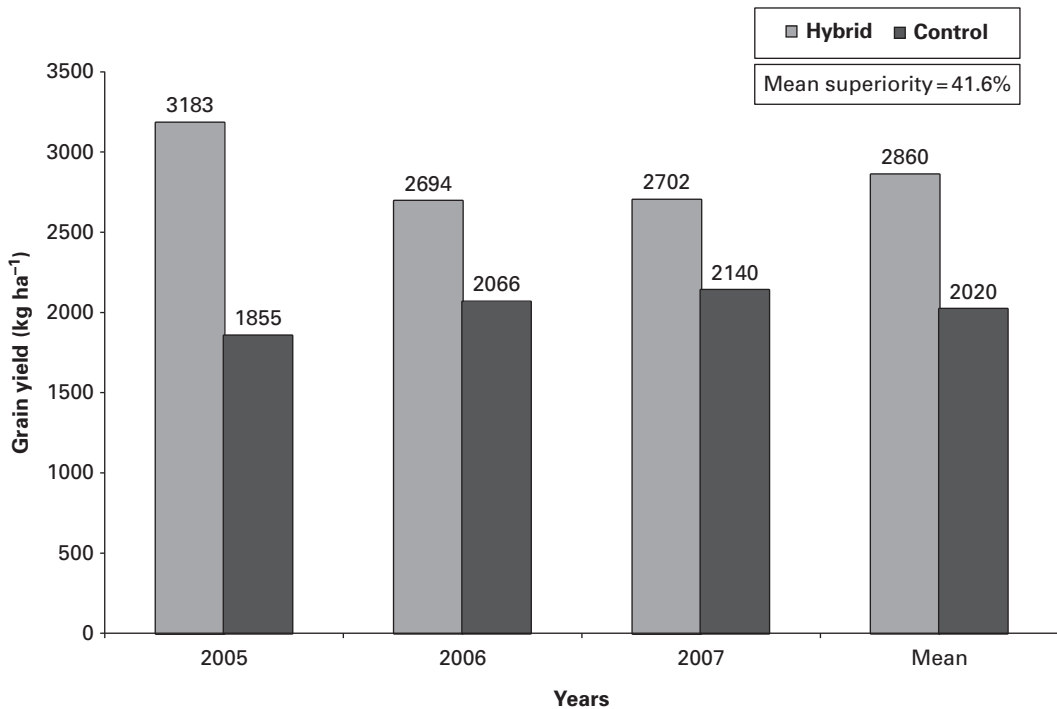


Figure 16.2. Performance of ICPH 2671 over three years and 21 locations in India.

4 Germplasm conservation, management, and utilization

The genebank at ICRISAT conserves 13,632 accessions of pigeonpea collected from 74 countries. India is the major contributor, with over 9,000 accessions. This is the single largest collection of pigeonpea germplasm assembled at any one place in the world. Landraces predominate the collection (8,215) followed by breeding materials (4,862) and wild relatives (555). ICRISAT has characterized, evaluated, and documented about 95% of the cultivated germplasm accessions. However, very few germplasm lines have been used by plant breeders.

To overcome the obstacle of so many accessions, which may be inhibiting the use of the collection by breeders, scientists at ICRISAT developed a “core collection”, consisting of about 10% of the entire collection, but representing the genetic variability of the entire collection (Reddy *et al.* 2005). However, it soon became evident that developing core collections will not solve the problem of low use of germplasm, as even the size of the core collection would be unwieldy for exploitation by crop improvement scientists. To overcome this, ICRISAT scientists (Upadhyaya and Ortiz 2001) proposed a “mini core collection” that contains 10% of the core or *c.* 1% of the entire collection and represents the diversity of the entire collection (Upadhyaya *et al.* 2006b). Owing to its greatly reduced size, the mini core collection provides an easy access to the germplasm

collection and scientists can evaluate the mini core collection easily and economically and identify trait-specific germplasm for use in their crop improvement programs (Upadhyaya *et al.* 2006a). A global composite collection of pigeonpea that included the mini core collection has been genotyped using 20 SSR markers, and a reference set of the 300 most diverse accessions has been selected and used in genomics studies. Systematic characterization and evaluation of germplasm accessions has resulted in the identification of several useful and new genotypes that have gone into the release of several varieties across the world.

5 Future

During the past 35 years, scientists have made significant contributions towards global pigeonpea research and development. Some of the constraints in the traditional landraces have been corrected, and these varieties are tailored to suit different cropping systems and new niches. ICRISAT maintains the world pigeonpea germplasm for present and future use. Further characterization of germplasm using molecular marker technology and greater sharing of pigeonpea germplasm with NARS partners needs to be done for better utilization of genetic resources.

While many biotic constraints such as *Fusarium* wilt and sterility mosaic diseases have been addressed, diseases such as *Phytophthora* blight are becoming important. New races of wilt and sterility mosaic are beginning to appear. These developments may be driven by climate change. The resistance levels of some wilt and sterility mosaic-resistant varieties are breaking down under new races of pathogens, and/or due to migration of races in newer geographical locations. Although a few sources of resistance towards *Fusarium* wilt, sterility mosaic, and *Phytophthora* blight are known, new sources of resistance need to be identified and introgressed in the pure lines and hybrid parental lines. Characterization and monitoring of the new races of wilt and sterility mosaic will be crucial towards development and deployment of the new varieties and hybrids. The evasive *Helicoverpa* resistance needs to be addressed through transgenics with optimized gene constructs with better temporal and spatial gene expression. We also need to breed for resistance to pod fly and *Maruca*, as these two pests are gaining importance in the wake of changing climate.

The new CMS-based hybrid technology calls for generating hybrids that combine high yield with resistance to major biotic and abiotic stresses. Resistance to major diseases (*Fusarium* wilt, sterility mosaic, *Phytophthora* blight), pests (*Helicoverpa*, pod fly, *Maruca*), drought, and salinity needs to be combined in the hybrid. This will require an enormous amount of research and cross-synergy in the fields of plant breeding, genetics, genetic engineering, genomics, and social science.

ICRISAT has demonstrated the power of partnership involving both private sector and government organizations. This approach exploits complementary expertise from various public and private partners in popularizing hybrids and pure-line varieties for the benefit of resource-poor farmers.

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Section IV

Traditional Management of Biodiversity

Stephen B. Brush

The contributions to this section deal with the connection between biological diversity in agriculture and its social, cultural, and geographic contexts. Crop evolution is generally understood through the processes of domestication that generated cultivated species and allowed the transformation of human life ways. Domestication set the stage for the transformation of subsistence and human social systems. The success of this transformation required not only new species of plants and animals but also a suite of allied technologies, organizational innovations, and behavioral change. The establishment of agricultural systems involving technology, social and economic organization, and cultural patterns was no less an accomplishment than crop domestication in the transformations that emerged at the end of the Pleistocene.

While the origins of agriculture through the processes of domestication and organization of food production systems loom very large in the evolution of crops and human society, both crops and agricultural systems have continued to evolve, and this evolution is significant to such concerns as the conservation of biological diversity and to meeting future needs such as those posed by climate change. Crop evolution after domestication is marked by such things as diffusion and adaptation to new habitats and the diversification of cultivars. The evolution of agricultural systems is marked by the elaboration of human knowledge systems about cultivated plants, change in social organization such as the elaboration of hierarchy, and dynamic economic organization for the allocation of resources and the distribution of production.

The chapters in this section include contributions from geographers ([Chapters 20 and 21](#)), ethnobotanists ([Chapters 18 and 19](#)) and plant ecologists ([Chapter 17](#)), and the topics covered by these chapters demonstrate the breadth of the field. An effort to understand agriculture in its landscape is common to all of the chapters, although the landscapes dealt with vary widely. A major cross-cutting theme is the interplay between physical attributes of agricultural systems and human adaption through managing different components in the

agricultural system. Equally important to these studies is complexity in agricultural environments and the impact of this complexity on both crops ([Chapters 17, 18, and 21](#)) and the human response ([Chapters 19 and 20](#)). The landscapes in focus here offer different but equally daunting challenges to agricultural production. Mountainous landscapes, described in [Chapters 18, 19, and 21](#), offer a mosaic of small and often drought-prone environments that are subject to degradation, such as soil erosion. The tropical lowland environments of Yucatan ([Chapter 20](#)), South America ([Chapters 17 and 19](#)), and the tropics of West Africa and Papua New Guinea ([Chapter 17](#)) are equally problematic to agriculture, for instance because of their soils. The collapse of the Maya civilization discussed in [Chapter 20](#) is, perhaps, the best-known example of the fragility of tropical agriculture.

These chapters explore two of the many modes of human adaptation to complex and problematic agricultural environments. The first is by managing and maintaining biological diversity within and among cultivars ([Chapters 17–19 and 21](#)) and the second is managing the architecture of production systems ([Chapters 20 and 21](#)). The chapters all note that human adaptation via these modes to complex and challenging production environments help us not only to understand the success and failure of agriculture but also to conceive of ways to confront a future that will be equally complex and challenging. A recurring idea that emerges here is that local knowledge and management by farmers, whether of biological diversity, irrigation, or soils, will be significant assets for meeting the challenges posed by climate change.

17 Ecological Approaches to Crop Domestication

D.B. McKey, M. Elias, B. Pujol, and A. Duputié

Understanding evolutionary adaptation of crop plants requires understanding the ecology of their wild ancestors¹ and the selective pressures that cultivators exerted when they began manipulating plants and shaping agricultural environments. For most plants, especially the diverse clonally propagated crops, we have only a broad-brush picture of the evolutionary ecology of domestication. Detailed investigations of crop wild relatives are rare, as are studies that take into account the full complexity of cultivated environments, from altered ecosystem processes and selective mechanisms to biotic interactions of crop plants with parasites and mutualists. The most important mutualists are the cultivators themselves, and an important part of the biotic environment of crop plants – what happens inside farmers' heads – has sometimes been neglected. Ecology – the interactions among cultivators, plants, and environments – has shaped the process of domestication. It continues to provide insights into ongoing processes of domestication today, in settings as diverse as landrace populations and biotechnology laboratories, and can inform strategies for managing the biodiversity of crop plants and their wild relatives.

In this chapter, we develop major themes in the evolutionary ecology of domestication. We show that evolution under domestication can contribute important insights into general questions in evolutionary ecology. We argue that much is to be gained from a broadening of domestication studies beyond their current focus on evolution in cereals and grain legumes, to encompass the great diversity of plants that cultivators have manipulated over the past 10,000 years, in what is the world's longest-running selection experiment (Gepts 2004).

The chapter is organized into four sections. First, we describe how domestication studies have served as a window into evolutionary processes, and analyze the crucial role of ecology in this exploration. We discuss the ecological context in which domestication took place, showing that understanding the evolution of domesticated plants depends on understanding how humans domesticate environments. In the second section, which comprises the bulk of the manuscript, we focus on a large group of plants that have been particularly neglected in

domestication studies: clonally propagated crops. We show that the principal reasons for our poor understanding of their evolution under domestication are our fragmentary knowledge of the biology and ecology of their wild relatives, preventing an appreciation of trait evolution, and a poor understanding of the reproductive ecology of the domesticates themselves, clouding our notions of how evolution in their populations might proceed. We illustrate these points with three crops: manioc, guinea yams, and bananas. These cases exemplify the great diversity of ecologies represented among the wild relatives of clonally propagated domesticated plants, the corresponding diversity of traits that have evolved under domestication, and the selective mechanisms responsible for trait evolution. In two short final sections, we discuss promising directions in crop ecology. We first show that domestication studies offer underexploited opportunities as tractable models for attacking some fundamental questions in evolutionary ecology, such as ecological speciation and evolution in (partly) clonal populations, and then discuss new applications of ecology in crop improvement and management strategies.

1 Domestication studies as a window into evolutionary processes

Ever since Darwin, domesticated plants have served as models for studying many questions of broad interest in evolutionary biology (Gepts 2004). Their rapid evolution, and the fact that their wild ancestors usually still exist and often can still be crossed with them (Ellstrand *et al.* 1999), facilitate comparative and experimental studies of evolution. However, the analysis of evolution under domestication appears to have captivated geneticists more than it has ecologists. Indeed, domesticated plants offer choice material for questions at the frontiers of evolutionary genetics, such as the genetic basis of traits, the evolution of development, and the architecture of genomes (Ross-Ibarra *et al.* 2007). In contrast, evolutionary ecologists have shown much less interest in domestication as a model, possibly because selective pressures imposed by farmers and by agricultural environments seemed to them to be straightforward and easily understood. Most of the seminal insights we have gained into the ecology of crop domestication have been contributed not by “card-carrying” ecologists, but by agronomists (Harlan 1992), archaeologists (Hillman and Davies 1990), and geographers (Blumler 1996). A more comprehensive ecology is required to fill important gaps in our understanding of the ecological aspects of domestication.

1.1 The importance of ecology in domestication studies

Ecology has a role to play in many aspects of domestication studies. First, it helps explain why some plants possess traits that made them easier to domesticate than others, and why such plants were more likely to be found in some regions than in others (Diamond 2002, Gepts 2008). Ecology is also crucial to explanations of the

evolutionary processes acting during domestication. In wild plants intensively harvested and managed by people, much artificial selection can take place before “cultivation”. Analysis of such incipient domestication (“*in situ* domestication” [Casas *et al.* 2007]) depends on a fine understanding of the plant in relation to its environment. Ecology also has shaped the traits of wild relatives and how they evolve under domestication, as examples presented here will develop in detail. Finally, ecology may constrain how rapidly domestication occurs. In one well-known case, the evolution of wheat, models based on knowledge of the genetic basis of traits associated with the domestication syndrome such as nonshattering panicles, and on the frequency of nonshattering mutants in wild populations, suggested that this and other domesticated traits should have evolved rapidly, over a few generations (Hillman and Davies 1990). Archaeological evidence, however, showed that the transition to domestication took over a thousand years (Tanno and Willcox 2006). Investigation of the structure of domesticated environments is helping to resolve this paradox. With harvesting techniques and field-tenure practices likely employed by many early farmers, and with their continued forced reliance on gathering wild seeds when crops failed, self-sown seeds (from shattering panicles) continued to contribute to harvests – and to the genetic composition of crop populations – for many generations, slowing the evolution of domesticated traits.

1.2 Domestication of plants, domestication of environments

People began domesticating environments long before they began cultivating plants (Yen 1989), but cultivation led to environmental changes even greater than those that preceded it. Agricultural environments often present strong ecological contrasts with the environments in which the wild progenitors of crop plants grow (Denison *et al.* 2003). Farmers endeavor to grow their crops in the resource-richest habitats available, to supply their crops with limiting resources, such as water, nitrogen, or mineral nutrients, and to protect their crops from herbivores and pathogens and from disturbances such as fire. One way of achieving these goals is by managing crop phenology. Farmers can synchronize planting and harvest time in ways that satiate predators of sprouting plants or seeds (Lansing and Miller 2005). They can also time agricultural cycles to adapt to seasonally changing environmental constraints. Domesticated plants thus often begin their life not only in highly favorable microsites but also – owing to a combination of reduced dormancy of domesticates and farmer choice of when to plant – at times when risk of fire, drought, or other stresses is minimal. Farmers also choose resource-rich environments and modify them to make them even richer. The extent to which farmers modify habitats is often truly astounding. Taking advantage of the nutrient-retaining capacities of charcoal, pre-Columbian farmers in Amazonia created *terra preta* soils whose nutrient status greatly surpasses anything seen in the region’s zonal soils, which are highly weathered, acid and nutrient-poor oxisols and ultisols (Glaser and Woods 2004).

Changes produced by domestication of the environment condition trait evolution in domesticated plants. Theory developed for wild plants, and well supported by data, emphasizes trade-offs between traits that confer rapid growth and those that confer tolerance to stresses associated with nutrient scarcity (Reich *et al.* 2003). Selection on plants living in resource-rich environments favors traits augmenting the plant's ability to acquire resources, whereas in resource-poor environments selection favors traits allowing the plant to conserve hard-earned resources. Following the same reasoning, the environmental changes associated with domestication should favor resource-acquisition strategies, compared with resource-conservation strategies of wild relatives. Much of the increased yield observed under domestication and crop improvement can indeed be ascribed to evolution driven by such trade-offs (Denison *et al.* 2003), and as will be developed here, such a shift in strategy appears to be one of the dominant themes of the evolutionary ecology of domestication.

Some crops are more “resource-conserving” than others. Manioc (*Manihot esculenta* Crantz) is prized for its ability to produce viable yields even under marginal conditions of water and nutrient availability. In resource-poor environments, maintaining yield requires resource-conserving traits, and some of these, such as chemical defense, have been retained, and possibly even enhanced (McKey and Beckerman 1993), during domestication of manioc. Different varieties of crop plants may also occupy different positions along the resource conservation/acquisition continuum. In manioc, “sweet” varieties with nontoxic roots may have higher yields in rich soils, or if herbivores and pathogens are absent, while “bitter” varieties with toxic roots give higher yields in poor soils (McKey and Beckerman 1993, Wilson 2008), especially if potential enemies are abundant. Ecological strategies show variation even among bitter manioc varieties: “fracas” varieties characterized by rapid production are adapted to richer alluvial and *terra preta* soils, while “forte” varieties, slower to produce but more resistant, are adapted to the poorest soils (Fraser and Clement 2008). Finally, in some regions, such as the semi-arid Sahel region of Africa, resource availability to crops varies dramatically among years. In at least two crops of this region, pearl millet (*Pennisetum glaucum* [L.] R. Br.) and sorghum (*Sorghum bicolor* [L.] Moench), continued gene flow with wild relatives (Mariac *et al.* 2006, Barnaud *et al.* 2009) generates variation that may help farmers adapt to such unpredictability. According to a hypothesis first proposed by Pernès (1986), genes from wild relatives may contribute to the rustic (resource-conserving) varieties that are the best yielders in bad years. These examples could be particularly instructive in the search for plant breeding strategies to adapt to climate change.

Defense is a component of ecological strategies whose evolution under domestication merits particular attention. Ecological shifts to resource-richer environments are predicted to lead to relaxed selection for chemical and physical defenses, and the plant's investment in them could be reallocated to increase yield (Rosenthal and Dirzo 1997). Furthermore, humans select against toxic or digestion-inhibiting compounds in parts of plants they consume. Variation in

the ease with which toxin-free plants can be selected is thought (Diamond 2002) to help explain why some plants could be domesticated (e.g., almonds, in which cyanogenesis has a simple genetic basis) and others could not (e.g., oaks, in which the polygenic inheritance of tannins makes it impossible to select tannin-free acorns). However, the balance of selection pressures could well favor the maintenance of defenses in many agricultural environments. First, resource availability varies even within agricultural environments. It is interesting that two crops that have maintained conspicuous defenses – manioc, which is cyanogenic, and grasspea (*Lathyrus sativus* L.), which contains neurotoxins – are both considered as being particularly adapted to marginal conditions where few other crops can produce viable yields (McKey and Beckerman 1993, Vaz Patto *et al.* 2006). Second, while greater resource availability in agricultural environments often does favor relaxed defenses, their species diversity is also usually lower than in the environments of their wild relatives, making them more apparent to herbivores and weakening other mechanisms of associative resistance, such as indirect defense provided by assemblages of natural enemies of herbivores, assemblages supported by the diverse resources of species-rich plant communities. Maintaining chemical defenses could be particularly important in herbivore- and pathogen-rich tropical agroecosystems, in extensive systems such as long-fallow swidden cultivation where crops are far from villages (where human presence dissuades some vertebrate herbivores), and in crops where edible organs such as leaves or tubers are potentially available to herbivores for long periods of their development. Synchronously ripening grain crops can be more easily protected from birds and other pests when most vulnerable, at maturity. Faced by such selective pressures, farmers have often retained varieties that contain anti-nutritional substances, adopting processing techniques that enable them to detoxify these built-in pesticides. Bitter manioc (McKey and Beckerman 1993, Wilson and Dufour 2002), grasspea (Butler *et al.* 1999), and tannin-rich red sorghum are the best-known examples, but others are known among both tuber and grain crops (Johns and Kubo 1988).

2 Integrating clonally propagated crop plants into domestication studies

The evolutionary ecology of clonally propagated crop plants is in general poorly understood. This is a huge gap in knowledge, because they include a large number of economically important plants. For example, nine of the world's 24 top crops in terms of tonnage harvested (Myers 1985) are clonally propagated: potato, sweet potato, manioc, grapes, sugarcane, bananas, oranges, apples, and yams. Collectively, clonally propagated crops represent tremendous phyletic, morphological, and ecological diversity. Even considering only a small number of globally or regionally important crops, they represent a host of families of both monocots (Araceae, Dioscoreaceae, Musaceae, Poaceae, Zingiberaceae, and others) and dicots (Euphorbiaceae, Moraceae, Oxalidaceae, Piperaceae, Solanaceae, and

many others) and diverse life forms including herbs, shrubs, trees, and vines. Direct human selection has acted on a great diversity of plant structures that are either consumed (roots, tubers, stems, leaves, fruits, and even seeds) or used to propagate the plant (rhizomes, stolons, corms, stems, underground, and aerial tubers). Indirect selection has undoubtedly acted on many other structures.

Why is the evolutionary biology of these crops so poorly explored? We believe there are two main reasons. First, our poor knowledge of the biology and ecology of their closest wild relatives prevents an appreciation of what traits have evolved. Part of the problem is their very diversity. Our ideas about evolution under domestication are primarily based on studies of seed-propagated crops belonging to only two plant families, Poaceae and Fabaceae, in which domestication has been characterized by widespread parallel evolution of similar traits, the classical features of the “domestication syndrome” such as the loss of mechanisms of seed dispersal and seed dormancy, and the reduction of branching. The obvious parallel and convergent evolution of crops in these families has stimulated comparative approaches that have led to many exciting discoveries about the genetic basis of traits (Doebley 2004, Ross-Ibarra *et al.* 2007). In contrast, the taxonomically and morphologically diverse clonally propagated crops do not seem to be characterized by any readily identifiable common domestication syndrome. As a group the wild relatives of these crops have very diverse ecologies and often quite unusual growth strategies, which have not always been appreciated by agronomists. This overwhelming diversity, and the lack of appreciation of complexity in the ecology of wild relatives, have hindered our ability to identify traits that have evolved under domestication, to understand why they have evolved, and to study their genetic basis.

Second, an incomplete understanding of the reproductive ecology of the crops themselves has clouded our ideas about how evolution in their populations might proceed. In an update of a classical 1984 essay comparing the reproductive systems of seed-propagated and clonal crops, Zohary (2004) stated that “in terms of selection, domestication of clonally propagated crops is largely a single step operation. With the exception of rare somatic mutations, selection is completed once a given clone is picked up.” He added that clonal crops “frequently underwent only a few recombination-and-selection cycles” and that “in terms of basic ecological adaptations they remained relatively close to their wild progenitors”. Referring to bananas (*Musa* spp.), Heslop-Harrison and Schwarzacher (2007) wrote: “Most of the cultivars are wild collections made by farmers of spontaneously occurring mutants with parthenocarpic fruit production, which were brought into cultivation and then multiplied and distributed by vegetative propagation.” Similarly, in a popular article about the same crop, one reads that “hunter-gatherers must have discovered rare mutant plants that produced seedless, edible fruits” (Pearce 2003). In our experience, the notion that clonal crops were “instantly domesticated” by the capture and clonal multiplication of mutant wild individuals is widely held. Many students have probably thought that studying such a simple event – as opposed to a process of some

complexity – was not very exciting and offered little basis for a career. We take issue with the notion of “instant domestication” on three points. First, the origin of the “spontaneously occurring mutants” (somatic mutations or new mutations in individuals from seed?) is often unspecified. Second, we believe such notions ascribe too much importance to recurring mutations and too little importance to recombination of previously existing alleles (see Pickersgill [2007] for a general discussion of this question in domestication studies). Third, generalizations about the paucity of recombination-and-selection cycles in clonal crops (Zohary 2004) are based primarily on studies of Mediterranean fruit trees. They appear less applicable to a large number of tropical clonal crops. In several such crops it has been demonstrated that reproductive systems are not strictly clonal, as usually thought, but mix clonal and sexual reproduction, so that populations have undergone repeated recombination-and-selection cycles, permitting the accumulation of domesticated traits often strikingly different from those of their closest wild relatives.

2.1 Reproductive systems and the evolutionary ecology of clonally propagated crop plants

Why have farmers chosen to propagate some plants clonally and others by seeds? Zohary (2004) pointed out that, in contrast to most seed-propagated crops, which are mainly autogamous (maize, pearl millet, and barley are conspicuous exceptions), clonally propagated crops are primarily outcrossers. Such plants do not breed true to type; clonal propagation enabled farmers to selectively multiply favorable new phenotypes. Alternative ways to achieve the same result would be to select for increased selfing ability (Gepts 2004), or for tighter linkage of domesticated traits (Le Thierry d’Ennequin *et al.* 1999). Clonal propagation also has other agronomic advantages, such as the more rapid growth and greater survivorship conferred by the larger propagules associated with this mode of reproduction.

Many clonally propagated crops appear to have reduced fertility (Zohary 2004). It is sometimes unclear whether it is the plant’s ability to reproduce sexually that has been diminished, or only the opportunity to do so, because of harvesting before flowering (Hather 1996) or other causes, such as mate limitation (see the banana case below). Still, reduction of sexual fertility is often considered a general evolutionary trend in these plants (Zohary 2004), and sexual fertility has been completely lost in some crops (*e.g.*, kava, *Piper methysticum* G. Forst. [Lebot *et al.* 1992]).

A selective pressure often proposed to account for reduction or loss of fertility is a trade-off between yield and the production of flowers and fruits. Plants that invest less in sexual reproduction may have increased yield of the plant part that is consumed, and farmer selection for high-yielding plants may automatically select for reduced production of flowers and fruits, unless these are the parts consumed, as in bananas and some varieties of taro. In what could be a frequent

scenario, interspecific hybridization could produce plants that exhibit both heterosis and sterility, each contributing to increased yield.

Although virtual loss of sexual fertility characterizes some domesticates, such as kava and most varieties of banana, it is far from being a universal trait of clonally propagated crop plants. Many retain a capacity for sexual reproduction that is far from “residual”, and as we show below, sexual reproduction plays an important role in the evolution of populations of these crops that are managed dynamically by farmers today. It continues to be important because cultivators are interested in its products and carefully observe plants originating from sex, incorporating some of these volunteer plants from seed as new clones.

What we know about trait evolution under domestication of these plants strongly suggests that sex and recombination also played a crucial role in their initial domestication. Where detailed studies have been conducted, as in manioc (see below), it is clear that domesticates of these plants differ in numerous genetically independent traits from their wild relatives. These differences have evolved over no more than the past 10,000 years (Gepts 2004). Such rapid evolution is difficult to square with limitations to evolution in purely clonal populations (Barton and Charlesworth 1998). Where somatic mutations are the only source of new genetic variation, deleterious mutations accumulate, reducing performance (and thereby fitness, if farmers prefer high-performing plants). Favorable mutations are rarer. By creating a great diversity of genotypes, recombination allows selective elimination of those with large numbers of deleterious mutations, and conservation of those that unite several favorable mutations, so that they cooperate within lineages rather than compete among lineages, increasing the rate of adaptive evolution. It is difficult to envisage how numerous genetically independent traits could be assembled in the absence of such recombination-and-selection cycles.

Sexual reproduction in these crops is integrated into a mixed clonal/sexual reproductive system, in which clonal propagation maintains favorable phenotypes at high frequency and recombination generates a diversity of genotypes, a few of which are highly selectively incorporated as new clones. Such a system combines the advantages of each reproductive pathway (maintenance of agronomic performance in a population dominated by selected clones, maintenance of adaptive potential by sex) while minimizing their respective disadvantages.

As we will show, in such mixed clonal/sexual systems, how and when selection acts, and what traits are affected by it, all depend on the ecology of the crop being considered and how it is managed by people. The ecological and morphological diversity of clonally propagated crops, and the diverse ends to which they are manipulated by cultivators, mean that the results of evolution, in terms of the kinds of traits that are modified, and how they are modified, show much greater diversity among clonal crops than among seed-propagated crops. We will illustrate this with three cases. We will first summarize findings for the best-studied case, that of manioc, and then present information on two less-studied cases, the guinea yam of Africa (*Dioscorea cayennensis*/*D. rotundata* species complex) and the

banana. These three plants contrast strongly in growth form and ecologically important traits of their wild relatives, and in the traits selection has favored under domestication.

2.2 The evolutionary ecology of manioc

Manioc is the clonally propagated crop whose evolutionary ecology has been most thoroughly investigated, largely in studies conducted by our group at Montpellier. The account given here draws heavily on a recent review of this work (Rival and McKey 2008). We first summarize the biology of the crop's closest wild relatives, showing how it has conditioned the ecology of the crop under traditional cultivation systems. Following this, we describe the patterns in the genetic diversity of landraces that initially suggested the importance of continuing recombination-and-selection cycles in the domestication of this plant. We then describe the functioning of the crop's mixed clonal/sexual reproductive system, better understood for manioc than for any other crop. Finally, we show how the selection pressures documented in contemporary crop populations can account for the evolution of the plant's traits during initial domestication.

2.2.1 Traits of the closest wild relative and the domestication syndrome

Manioc's closest wild relative, *M. esculenta* subsp. *flabellifolia* (Olsen and Schaal 1999), is a plant of forest/savanna ecotones distributed around the drier seasonal rim of Amazonia. Among its adaptations to ecotone environments are tuberous roots, underground reserves that enable rapid regrowth after fire or other disturbances. They also show plasticity in growth form. Much-branched shrubs in open environments, they persist as scandent vines as vegetation closes during succession. They also possess several adaptations allowing rapid regeneration from a soil bank of dormant seeds following a new disturbance. Their two-stage seed dispersal system features ballistic autochory (explosively dehiscent capsules) followed by myrmecochory: each seed bears an elaiosome (a food body rich in lipids and other nutrients) that attracts ants (Elias and McKey 2000). Ants carry diaspores to nests, where the elaiosome is fed to the brood. Seeds are then discarded in a refuse pile near the nest, where they become buried at varying depths in the soil. Thus protected, they can lie dormant for years (seeds from which the elaiosome has been removed are perfectly capable of germinating [Pujol *et al.* 2002]). Seeds of manioc's wild relatives use soil temperature as a germination cue. At temperatures typical of vegetation-shaded soils in the lowland tropics (25°C) they remain dormant, but when soil temperatures of 35°C or more signal that vegetation cover has been removed by a disturbance, they germinate, if ample water is available (Pujol *et al.* 2002). These features of seed and seedling biology have been inherited largely intact by domesticated manioc.

Other traits of the domesticate, however, have diverged from the wild relatives. These include of course traits directly selected by humans, such as the size and production of tuberous roots and traits facilitating clonal propagation via stem

cuttings. For example, reduction in the extent of branching results in thicker stems, producing clonal propagules that have more reserves and are less subject to desiccation (Jennings 1995, Schaal *et al.* 2006). However, the domesticate has also diverged from the wild relative in traits only indirectly selected: leaf tannin content has undergone reduction (Mondolot *et al.* 2008) and several leaf traits have led to higher mass-based photosynthetic rates in domesticated manioc (Pujol *et al.* 2008). Finally, and most curiously, domesticated manioc and its wild ancestor differ in seedling morphology (Pujol *et al.* 2005b). Domestication of this crop by Amerindians over the past 10,000 years thus involved the assembly of a large number of independent traits, not something that would be easily accomplished under purely clonal evolution.

2.2.2 The nature of landraces and landrace diversity in a clonally propagated crop

A brief walk in a manioc plantation of Amerindian cultivators in Amazonia raises further questions about the origin of diversity in this “clonally” propagated crop. The number of different named categories, i.e., landraces (varieties as they are named and recognized by cultivators), present in the fields of a single village can surpass 100 (Boster 1983, Duputié *et al.* 2009). Common-garden experiments show that despite environmental effects on traits, these different landraces are also phenotypically distinct, each possessing particular combinations of independent traits, such as the extent of branching, the form of roots and their composition (starch content, toxicity [“sweet” vs. “bitter”]), and the color of different organs (Elias *et al.* 2001a). The structure of trait variation indicates not diversification within purely clonal lineages, but frequent recombination. Genetic analysis confirms this impression. Phenotypic diversity is underlain by great genetic diversity, and landraces are genetically differentiated. Most strikingly, most landraces do not correspond to a single clone. Although one or two clones may be numerically predominant, a landrace is usually constituted of groups of genotypes that are derived from distinct recombination events but share similar phenotypes (Elias *et al.* 2000b, 2001b). Sex thus appears to continue to play an important role in the structure of diversity. Furthermore, because farmers plant numerous distinct landraces in a single field (Elias *et al.* 2000a, Duputié *et al.* 2009), there is enormous scope for continued recombination.

2.2.3 How sex enters the game

Like most other clonally propagated crop plants, manioc is primarily outcrossing (David *et al.* 2007), although self-compatible, and the benefit of clonal propagation is seen in the genotypic composition of the predominant clones. Their high heterozygosity for neutral microsatellite markers – typical of both Amazonian (Elias *et al.* 2004) and African (Fregene *et al.* 2003) landraces – indicates genome-wide heterozygosity, signaling their origin from matings between unrelated plants and thus their relative freedom from inbreeding depression. Clonal multiplication enabled these “elite” clones to reach their high frequency. However, the rapid

evolutionary divergence of manioc from its wild relative is difficult to reconcile with evolution in a purely clonal reproductive system. The diversity of traits that evolved during the domestication of manioc suggests the action of repeated cycles of recombination (necessary to generate variation) and selection (to fix certain traits and maintain agronomic performance).

Sex gets into the system by the interaction between the biology of manioc and the actions of cultivators. The field–fallow cycles of swidden agriculture nicely take advantage of the reproductive traits manioc inherited from its wild ancestor. Seeds, dispersed by ants, are buried and remain dormant in the shaded soils throughout the fallow period. When a new field is opened, volunteer seedlings from this seed bank emerge in large numbers, their emergence coinciding with the period when cultivators plant stem cuttings (Elias *et al.* 2000a). Volunteer seedlings are closely observed by cultivators, who allow them to grow. Those that survive to maturity are harvested and their roots are processed. Farmers evaluate them and multiply some of them as new clones. Rarely, plants from seed are judged sufficiently novel to be multiplied as a new named variety. Much more frequently, they are incorporated into the stock of clones of a named variety they resemble, explaining the polyclonal nature of these varieties (Elias *et al.* 2000a). As in many other crops, cultivators increase the diversity of material upon which recombination and selection can act by the frequent and widespread exchange of cultivars, both directly via exchange of stem cuttings in social networks (for an example see Elias *et al.* 2000a) as well as indirectly via soil seed banks (Pujol *et al.* 2007).

Mixing clonal propagation and sex is not as straightforward as it may at first seem. Two problems may arise: population structures created by clonal propagation may lead to frequent inbreeding; and crossing of highly differentiated clones may break up favorable trait combinations conserved in distinct landraces. Because the aim of clonal propagation is to multiply selected genotypes to high frequencies, many plants in a field are likely to be clonemates. Furthermore, in at least the three Amerindian groups we have studied (Makushi [Carib linguistic family] in Guyana and Palikur [Arawakan] and Wayãpi [Tupi-Guaraní] in French Guiana), cultivators tend to plant cuttings in monovarietal patches, so that a plant's neighbors are frequently clonemates. This clumping of clonemates affects the population's mating system. Because pollinators transport pollen mostly between neighboring plants, many seeds are the result of highly inbred matings. At the same time, cultivators usually plant several highly differentiated varieties in each field, and pollen transfer between them produces highly outcrossed offspring. The overall result of the peculiar spatial genetic structure of these polyvarietal populations is a highly unusual mating structure, with great variance in the extent of inbreeding. Given this diversity, it is clear that incorporation of plants from seeds as new clones must be highly selective if agronomic quality and favorable trait combinations are both to be maintained.

Detailed field studies in Palikur farms have shown that volunteer plants from seeds are subjected to high mortality, that this mortality is selective, and that while at least four different selective mechanisms operate at different times in the field cycle, they all have similar consequences for phenotypes and genotypes: selection

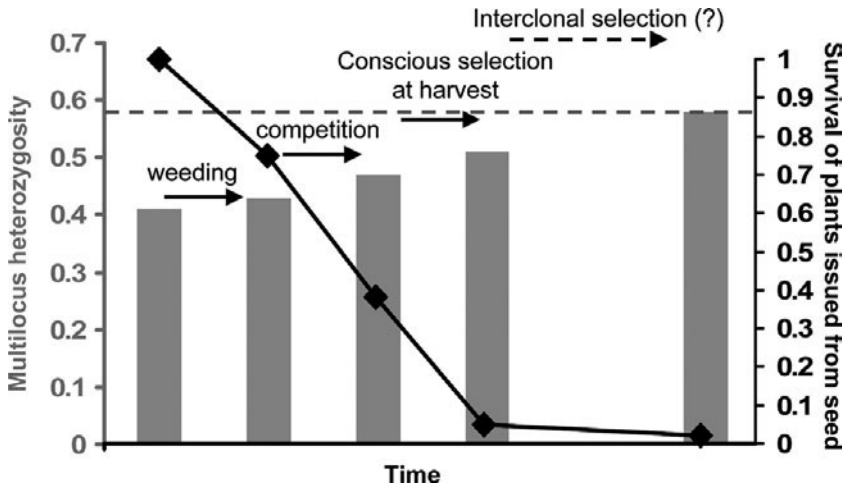


Figure 17.1. Stages in the selective incorporation, as new clones, of volunteer plants of manioc issued from seeds in fields of Amerindian cultivators. Seedlings appear in newly cleared fields, then steadily decrease in number until the field is harvested (black line). Selective mortality of inbred seedlings occurs in four stages. First, some are removed by farmers during manual weeding. Others die from “natural” causes, mainly intraspecific competition. At harvest, most are discarded. Finally, new clones that are incorporated undergo a trial period of several years, during which many probably disappear via interclonal selection (see Duputié *et al.* 2009 for discussion). At all four stages, inbred individuals are selected against, as shown by the increase in multilocus heterozygosity of surviving individuals over time (gray bars), until they eventually reach the average level of landraces (dashed line). Data for survival and multilocus heterozygosity are from Pujol *et al.* (2005a,b), Pujol and McKey (2006), and Duputié *et al.* (2009).

favors plants that grow rapidly, and these are the most outcrossed individuals. One stage of selective mortality occurs when farmers manually weed their fields several months after planting. Those plants that are removed are smaller (size is a good indicator of vigor because seedlings in a field are a single even-aged cohort) and more inbred than those that survive (Pujol *et al.* 2005a). Another stage of selective mortality is caused by intraspecific competition, mostly in the first year of growth. Competition is severe because ant-mediated seed dispersal generates clusters of seedlings. In these clusters, individuals with an initial size advantage win. They are also the most outbred (Pujol and McKey 2006). The third stage of selection occurs at harvest time, when farmers select large, vigorous plants for propagation. The fourth stage of selection was studied not among the Palikur but among the Wayãpi. Plants from seed selected for clonal propagation undergo a trial period, during which they are multiplied and managed separately from established clones of the same landrace. Clones under trial are more inbred than established clones (Duputié *et al.* 2009). From a strong heterozygote deficit at the beginning of the cycle, testifying to a globally inbred mating system, seedlings that survive these different selective processes progressively come to resemble established clones in their high heterozygosity and vigor (Figure 17.1).

The highly selective incorporation of products of sex injects genetic diversity, and thereby adaptive potential, while maintaining the population's agronomic performance.

How do cultivators deal with the other problem that arises in the mixing of clonal propagation and sex, the breakup of favorable trait combinations when highly differentiated landraces cross? Duputié *et al.* (2009) found that Wayãpi farmers selected not only against the most inbred plants but also against the most outbred. This result was attributed to ideotypic selection against “off-type” plants resulting from intervarietal crosses.

Studying the functioning of mixed clonal/sexual systems in contemporary fields of Amerindian cultivators opens a window into evolutionary dynamics throughout domestication. The picture that emerges from our studies – strong selection favoring rapidly growing plants – fits quite well with theory predicting that selection in agricultural environments should favor a move from the resource-conservation end of the allocation spectrum to a strategy emphasizing resource acquisition. The same selective forces that have favored outbred plants appear to have also driven selection for other traits leading to increased growth rates, such as leaf traits leading to increased mass-based photosynthetic rates (Pujol *et al.* 2008) and reduced foliar tannin contents (Mondolot *et al.* 2008).

2.2.4 An unexpected feature of the domestication syndrome

These forces also appear to be responsible for the most striking and surprising evolutionary change of manioc under domestication: the divergence from its wild relatives in seedling morphology and germination type (Pujol *et al.* 2005b). Seeds of manioc's closest wild relatives are characterized by hypogeal germination (Figure 17.2a). The hypocotyl does not elongate during germination, so that cotyledons remain buried in the soil. Enclosed in the testa, they serve as stored reserves. The epicotyl grows to the surface. The seedling's first photosynthetic organs are its first true leaves. In contrast, seeds of domesticated manioc exhibit epigeal germination (Figure 17.2b). The hypocotyl elongates, elevating the cotyledons above the soil surface. The cotyledons emerge from the testa and expand into foliaceous photosynthetic organs. This difference is truly remarkable. In forest trees, seedling functional morphology is evolutionarily highly conserved, often being invariant within a genus (Garwood 1996). In contrast, comparison of manioc and its closest wild relatives indicate that the domesticate has evolved a radically different germination type in less than 10,000 years. This evolutionary change is all the more surprising in that it has occurred in a clonally propagated crop plant in which sexual reproduction has until recently been thought to play an insignificant role.

However, this transformation can be explained by the selective pressures we now know to be operating in Amerindian manioc farms. Based on what is known about the strategies of forest trees (Kitajima and Fenner 2000), the seedlings of the wild relative should be much more tolerant of stresses such as drought, fire, or

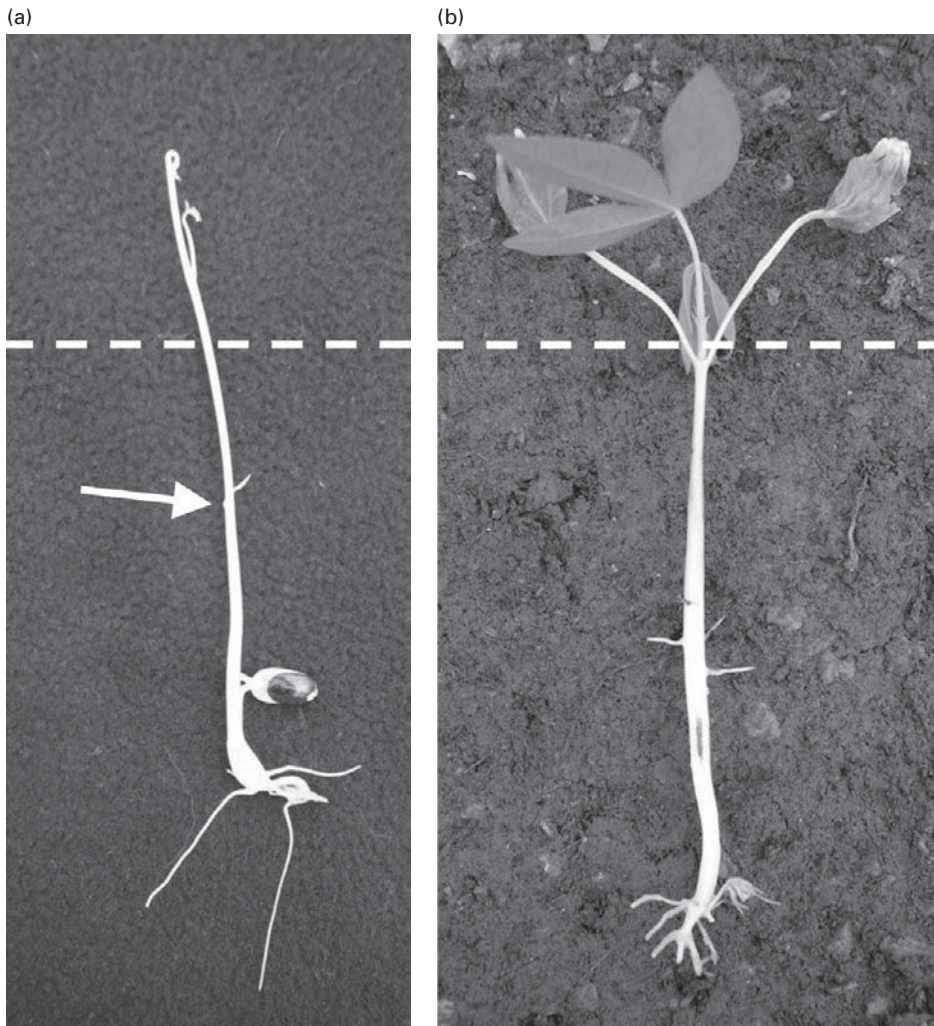


Figure 17.2. Morphology and germination strategies of seedlings of manioc closest wild relatives (a) and of manioc itself (b). The dashed line indicates the level of the soil. Pictures were taken about eight days after seed germination. Underground reserves in storage cotyledons and in the swollen hypocotyl and axillary meristems (arrow) on the underground part of the epicotyl, enable the seedlings of the wild relative to resprout if its aboveground parts are destroyed by drought, herbivores, pathogens, or fire. However, initial growth rate is slow, because photosynthetic surfaces (the first true leaves) are only slowly put in place. In contrast, the green, foliaceous cotyledons of seedlings of domesticated manioc quickly fuel more rapid initial growth, but the plant cannot resprout if its aerial parts are destroyed (authors' unpublished data).

herbivory to above-ground parts, for if these are destroyed the seedling has reserves (storage cotyledons) and meristems (axillary to cataphylls at nodes on the underground portion of the epicotyl) that permit resprouting. However, the seedling's tolerance to stress comes at the cost of a reduction in growth rate: its

initial photosynthetic surface, the tiny first true leaf, is much smaller than if the cotyledons had served as photosynthetic rather than as storage organs. The strategy of manioc's wild relatives emphasizes resource conservation. In contrast, the seedling of domesticated manioc should be intolerant of loss of its above-ground parts, for it has neither reserves nor meristems to resprout. On the other hand, its photosynthetic cotyledons confer rapid growth. The strategy of domesticated manioc thus emphasizes resource acquisition. Competition, ultimately mediated by human selection, appears to have outweighed potential hazards to seedlings. Although spectacular and surprising, the transformation of seedling morphology during domestication of manioc can be understood as one more trait that increases the growth rate of volunteer plants from seed, and the probability that they will attract the attention of farmers and become established clones (Pujol *et al.* 2005b).

One further aspect of the evolution of seedling morphology in manioc is noteworthy. The depth at which seeds are buried in soil is variable. They may sometimes be so close to the surface that cotyledons are exposed to light during germination. When this happens, seedlings of the wild relative adopt a morphology somewhat different than that described above. While the behavior of the hypocotyl is unchanged, the cotyledons emerge from the testa and become foliaceous (see Figure 1d in Pujol *et al.* [2005b]). This plasticity enables the plant to use its cotyledons for photosynthesis when their location at the soil surface precludes their serving as protected underground reserves. This plasticity probably facilitated the transformation to true epigeal germination in domesticated manioc. Interestingly, plasticity in this trait was apparently lost during domestication: the cotyledons of domesticated manioc seeds emerge and expand into foliaceous organs even under conditions of total darkness.

To summarize, our results show that the domestication of manioc involved divergence from the wild ancestor in numerous independent traits. Domestication was not a one-step event but a process of adaptation, and the assembly of so many traits must have required numerous recombination-and-selection cycles. Natural and unconscious selection played an important role, as shown particularly by the evolutionary transformation of seedlings, although farmers do not directly manipulate any facet of the plant's sexual reproduction. The process of domestication continues, and studying the dynamics of contemporary landrace populations gives clues about evolutionary mechanisms and selective pressures acting during initial domestication.

2.3 Evolutionary biology of domestication of the guinea yam

2.3.1 The ongoing domestication of yam in West Africa

The literature on domestication of the guinea yam (*Dioscorea cayennensis*/*D. rotundata* species complex) emphasizes a curious phenomenon termed “ennoblement”. Farmers are reported to transplant into their fields “wild” yams found in secondary forest (Chikwendu and Okezie 1989, Dumont and

Vernier 2000). Clonal derivatives of these plants are initially characterized by wild traits. Their tubers bear large, long thorns, are highly fibrous, and are irregular in shape, often long, branched, and deeply buried. Once plants are placed in cultivated environments and carefully managed, these and other wild traits disappear over several clonal variations (Chikwendu and Okezie 1989). Various techniques are employed. For example, some farmers place obstacles such as pottery fragments beneath the sett. Thus constrained, the plant produces a short, squat, shallow tuber that is much more easily harvested. After a few clonal generations of such treatment, the plant produces such tubers without requiring manipulation. The nature of this process, which seems to achieve “domestication” with little or no genetic change, has remained somewhat mysterious. Somatic mutations and epigenetic effects have been invoked to explain the process (see Tostain *et al.* 2003), but we know of no evidence favoring this hypothesis. Recent work by Nora Scarcelli and colleagues (Scarcelli *et al.* 2006a,b) has begun to shed light on the problem. Using diagnostic molecular markers, they found that although most of these “wild” yams were referable to the wild parent (*D. abyssinica* in savanna environments, *D. praehensilis* in forest environments; the two are likely conspecific ecotypes), some were wild $\times$ domesticated hybrids. Other accessions, which had successfully undergone ennoblement (termed “pre-domesticated” accessions by these authors), included not only hybrids but also recombinant domesticated genotypes. The work of Scarcelli and colleagues suggests that domestication, as in all other crop plants, did indeed involve genetic change, and that this process is ongoing. Furthermore, a plausible interpretation of the genetic difference between “wild” and “pre-domesticated” accessions is that individuals of hybrid and domesticated genotypes are more easily ennobled. In fact, attempted “ennoblement” is not always successful. Farmers consider some individuals as non-domesticable, judging that others are exploitable immediately and others only after several years of “ennoblement” (Chair *et al.* 2005). “Ennoblement”, sometimes abusively equated with “domestication”, may simply be the expression of extraordinary phenotypic plasticity in the domesticate, at least in the populations managed in this way by farmers. In fact, plasticity may be one of the traits most favored by selection.

2.3.2 A reproductive ecology presenting strong contrasts with that of manioc

In the context of this essay, the principal lesson to be drawn from this example is the great contrast in the ecology of sexual reproduction between the yam case and that of manioc in fields of Amazonian Amerindians. As in the manioc case, African cultivators regularly incorporate yam plants from seed as new clones. However, the ecology of seeds and seedlings is very different in these two plants, leading to fundamental differences in the process of their incorporation and in the kinds of traits favored by selection. The principal contrast in their ecology is that while plants from seeds of manioc pass their entire life, from seedling to mature

plant, in cultivated fields, plants from seeds of yam pass their early life in secondary forest, and are later transplanted into field environments. This should select for great phenotypic plasticity.

How can this difference between the two crops in life cycles of plants from seeds be explained? Seeds of *Dioscorea* are very small. Lacking dormancy, they germinate rapidly. Survival and growth of seedlings is highly dependent on light availability. The winged seeds are very light, and many are dispersed to secondary forest near cultivated fields. Because it takes several years for seedlings to develop to a size that would attract the attention of farmers, even those that fall into cultivated fields will probably not be targets for incorporation until long after the field has been left to fallow. Thus, in marked contrast to manioc, plants originated from seed are likely to spend the first years of their lives not in field environments but in secondary forest. Plants found by farmers and transplanted into fields have thus survived for several years in secondary forest. Once in the new field environment, a very different set of requirements is imposed on the plant. To satisfy the exigencies of farmers and thereby be incorporated and multiplied as new clones, they must produce large, shallow tubers that are easily harvestable. This life cycle, encompassing very different ecologies at different stages, appears to have maintained great phenotypic plasticity in a number of traits. Thus, depending on the reproductive ecology of the crop in question, domestication may result in either reduction of plasticity, as in the branching architecture of maize (Lukens and Doebley 1999) and the seedling morphology of manioc, or in its maintenance or even enhancement, as in the guinea yam. The ecological context in which traits of the domesticate are expressed appears to determine whether plasticity is adaptive or not.

2.3.3 Ecology and the domestication syndrome

What traits have evolved under domestication of this plant? Answering this question requires understanding the adaptations of the plant's closest wild relatives. One of these, the forest yam *D. praehensilis*, is characterized by one of the strangest ecologies we have encountered among wild relatives of crop plants, an evolutionary ecologist's dream but an agronomist's nightmare. Like many other yams of the section *Enantiophyllum*, *D. praehensilis* has a very unusual growth strategy (Figure 17.3). A geophytic vine of seasonal humid forests, the central feature in its life cycle is an annually repeated race to the forest canopy, fueled by reserves stored in an underground tuber (Di Giusto *et al.* 2001). Upon reaching the canopy, which may be at 30 m or higher, its aerial apparatus has a single season of photosynthesis to restock the reserves for next year's trip. After this single season of growth (about six months), the aerial apparatus dies to the ground. The tuber remains quiescent during the dry season, its reserves protected by their deep burial and by the presence of a "crown of thorns" – densely branched spiny roots – in superficial soil layers above the tuber. Just before the beginning of the rainy season, the race to the canopy begins anew. This heliophile cannot conduct net positive photosynthesis in the shaded understory, and how much the shoot system

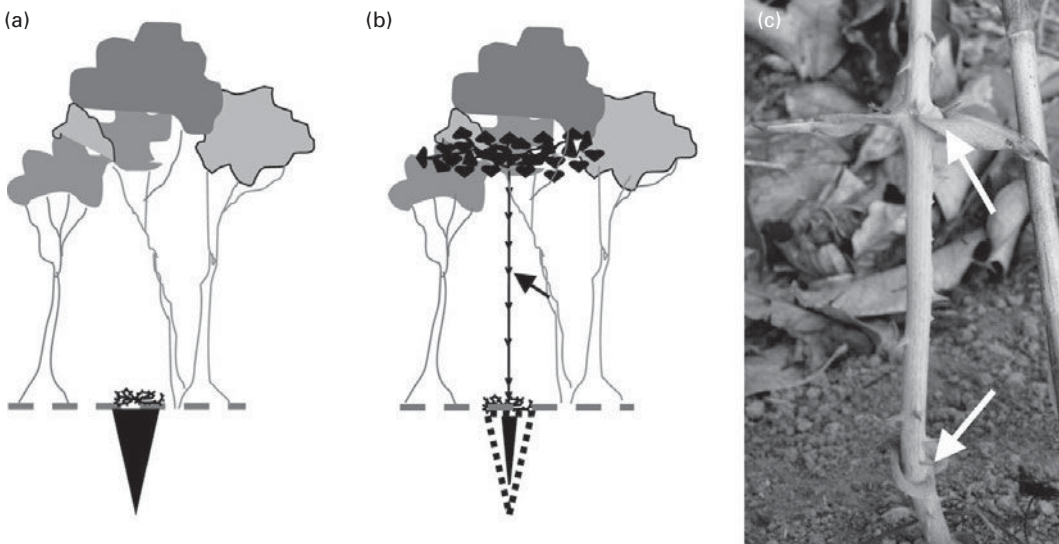


Figure 17.3. Growth strategy of *Dioscorea praehensilis*, a wild ancestor of the guinea yam, as studied in forests of southeastern Cameroon (DiGiusto 2002). The plant is a geophyte, i.e., the aerial apparatus dies to the ground each year, during the dry season (a). Its life cycle features an annually repeated struggle, using reserves stored in the underground tuber, to reach the forest canopy and by its photosynthesis during the rainy season (b) replenish the tuber reserves that will enable the plant to make the same trip the following year. While traversing the forest understory, the plant bears no true leaves, only cataphylls, indicated by arrows in (b) and (c). Axillary meristems are associated with each pair of cataphylls.

can produce in its single season of growth depends on how rapidly it reaches the canopy. Its morphology is thus adapted to maximize the rate of vertical growth. In the shaded understory, the plant does not branch: a single apical meristem assures stem height extension rates of up to 30 cm or more each day (DiGiusto 2002). Nor does the plant produce true foliage leaves at this growth stage. At each node are two opposite cataphylls (scale leaves), with associated axillary meristems that remain dormant as long as the apical meristem is active. Although this morphology allows rapid height extension, it has a conspicuous weak point: if the tender apical meristem, continuously present through this critical growth phase, is attacked by herbivores, this delays the shoot's arrival to the canopy. Field experiments conducted by Bruno DiGiusto (2002) showed that loss of the apical meristem leads to a delay of from 10 to up to 45 days in reaching the canopy, depending on when during its climb the apical meristem is attacked. One reason for the long delay is that, like other monocots, yams lack secondary growth. The small axillary meristem that takes over must first undergo establishment growth (Tomlinson 1987) to reach its definitive, unchanging primary diameter, which must be large enough to produce stems capable of supporting the plant's entire crop of leaves throughout the growth season. As expected from



Figure 17.4. An ant (*Polyrhachis* sp.) at extrafloral nectaries (darker-colored areas) on cataphylls of an apical meristem of *Dioscorea praehensilis* in a forest in southeastern Cameroon. Protection conferred by constant ant patrolling of the apical meristem during its long trip to the canopy is essential to the plant's success. Photograph courtesy of Bruno DiGiusto.

its important contribution to plant fitness, the apical meristem is provided with chemical defenses (saponins) against herbivores (DiGiusto *et al.* 2001). Nevertheless, meristems are attacked by herbivores, favoring the evolution of additional defenses. Here is where the significance of cataphylls is seen. Although morphologically reduced, they have a crucial function, because when young, each bears numerous extrafloral nectaries that secrete sugar- and amino-acid-rich nectar throughout the day and night, attracting ants to the apical meristem (Figure 17.4). Their presence dissuades most herbivores. However, one specialist herbivore, the chrysomelid beetle *Lilioceris latipennis* Clark, not only tolerates

the plant's chemical defenses, but also turns them against ants: larvae cover their body with a "fecal shield" containing slightly altered plant saponins. Although ants attack adult *Lilioceris*, reducing oviposition on the plant, and can kill early-instar *Lilioceris* larvae, if larvae escape long enough to reach a critical minimum size, they can no longer be killed or dislodged by ants. Constant patrolling is thus required for effective protection. The fate of apical meristems, and thus of the plant, depends on the balance of interactions between the plant, its herbivores, and ants.

From this ecologically complex starting material, what traits have evolved under domestication? This question is currently unanswerable, for two reasons. First, equating "ennoblement" with "domestication" has generated confusion, at least in our minds, about whether traits have been lost or whether their expression is conditioned by complex patterns of phenotypic plasticity. Several traits of the wild relative should be strongly counter-selected in domesticated environments. These include traits that make the tuber more difficult to harvest, such as deep burial and the "crown of thorns". The long phase of stem elongation without foliage leaves is no longer adaptive in cultivated environments, as it would reduce (or at least delay) production. However, these traits would continue to be adaptive in wild environments, where volunteer plants from seed spend the first years of their lives. Variation in these traits persists among cultivated varieties, particularly where farmers still practice dynamic management featuring the incorporation of volunteer plants from seed (Chikwendu and Okezie 1989). To what extent this variation reflects genetic diversity, or phenotypic plasticity, is quite unclear. Second, because agronomists have generally not appreciated the complex ecology of the wild relative, many ecologically important traits have largely escaped their attention. For example, we have uncovered no mention of the functional roles of cataphylls, only the observation that the number of cataphylls is reduced in domesticated yams (Chikwendu and Okezie 1989). Yams of the section *Enantiophyllum* thus present a number of intriguing traits that should be under divergent selective pressures in wild and domesticated environments, but whether they have evolved under domestication has been little explored, largely owing to our poor understanding of the ecological context of domestication.

2.4 Bananas: processes of domestication in a crop characterized by almost purely clonal reproduction today

The two previous examples illustrate the ecological diversity of clonally propagated crops. Their complex and strongly contrasting life forms and life cycles have led to great differences in the process of incorporation of volunteer plants from seed, and in the kinds of traits that selection favors under domestication. The third example, banana, is a crop in which many contemporary populations have virtually lost the capacity for sexual reproduction. Owing to our familiarity with the seedless fruits of today's widespread varieties, bananas and plantains exemplify

the popular notion (e.g., Pearce 2003) of crops evolving under purely clonal reproduction since their initial domestication. If such were the case, somatoclonal variation would be the main source of diversity. At local or regional scales, this may be true. East and West Africa each have distinctive banana types consisting of a cluster of local landraces, which appear to have resulted from evolution under virtually purely clonal reproduction (Pickersgill 1998, De Langhe and De Maret 1999). Whether there were one or more introductions of the crop into Africa, and when, are still controversial questions (Kennedy 2009). However, the almost exclusive predominance of clonal reproduction in many contemporary banana populations has tended to obscure our understanding of the crop's early evolution. As pointed out by Jean Kennedy (2009, Kennedy and Clarke 2004), most accounts of banana evolution under domestication give very little insight into the crucial early stages of human intervention. Mixed clonal/sexual reproduction played a key role in the origin and early diversification of the crop, and mixed clonal/sexual systems still operate in some domesticated banana populations today.

Wild *Musa* species are light-loving giant herbs that colonize disturbed sites in forest, such as landslides and treefalls (Simmonds 1962). Seed dispersal by frugivorous vertebrates is an important part of this ecological strategy. Whereas selection under domestication favored the evolution of seedless fruit (independently in two different sections of the genus), this was a complex process, not an event (Simmonds 1962). Sexual fertility was progressively reduced, but probably remained sufficiently high, over a long enough period of time, for recombination to assemble important domesticated traits. As pointed out by De Langhe and De Maret (1999), “both semi-wild [i.e., by seed] and vegetative propagation may have co-existed for a considerable time”.

Why did seedlessness take so long to evolve? First, selection against seediness may have been weaker than our current fixation on the edible fruit of this crop would lead us to suppose. Kennedy (2009, Kennedy and Clarke 2004) has emphasized the diversity of uses of different organs of the banana plant by many of its contemporary cultivators. Immature seedy fruits, corms, stems, and inflorescences are eaten; fibers of leaves and stems are used to make textiles. Edible fruits are not always the most important product of the plant, and this situation is likely to have been more frequent in the past. Second, seedlessness is frequently revealed to be due not to one trait but to a combination of traits – parthenocarpy and sterility (male, female, or both) – which themselves have been assembled by recombination. Parthenocarpy involves mechanisms at least partly independent of the loss of sterility (Simmonds 1962). Many so-called “archaic” edible banana varieties are in effect *facultatively* parthenocarpic, as emphasized by Kennedy (2009). Capable of producing fleshy, seedless fruit in the absence of suitable pollen, they can also produce seeded fruit if they are fertilized. In populations including such varieties, even the occasional incorporation of volunteer plants from seed could have a huge impact on the genotypic diversity of clones. In evolutionary terms, a little sex goes a long way (Halkett *et al.* 2005).

Observations among contemporary cultivators of facultatively parthenocarpic landraces give tantalizing clues into the ecology that may have characterized banana populations during much of their evolutionary history under domestication (Kennedy and Clarke 2004, J. Kennedy, pers. comm.²). In Milne Bay Province, Papua New Guinea, village elders express annoyance when favorite old-fashioned varieties produce increasingly seedy fruits. Worried that they may break their few remaining teeth (meaning that they would no longer be able to chew betel nut), the elders' crescendo of complaints eventually persuade the village's young men to search out and cut down, in forest fallow fringing their gardens, the wild *Musa* they perceive as being the source of the viable pollen. Such anecdotes suggest that the evolutionary ecology of banana is every bit as rich and as full of surprises as that of crops such as manioc and yams.

Ironically, the most extravagant events of outcrossed sex in bananas may have also sealed the end of recombination as a source of diversity in the crop. The seeds produced by facultatively parthenocarpic varieties when they are pollinated include diploid, triploid, and tetraploid interspecific hybrids. As in a number of clonally propagated crops, polyploidization through interspecific hybridization probably led not only to heterosis but also accelerated the suppression of fertility. Productive, sterile, seedless varieties, favored by multiple selective forces, put most populations of this crop onto the road of purely clonal evolution.

As publicized in a popular article (Pearce 2003), bananas appear to illustrate one of the predicted consequences of the loss of sex: the loss of evolutionary potential and thereby of the capacity to adapt to new pressures, particularly biotic pressures such as pathogens. Commercial banana production, based on a small group of clones with very little genetic diversity, has from the start depended on heavy application of agrochemicals, which may account for 30% of the production costs, and diseases are also responsible for steady yield declines in smallholder systems (Heslop-Harrison and Schwarzacher 2007). In terms of its evolutionary dynamics, the relationship between humans and bananas recalls the argument of Law (1988) that nurture of an asexual symbiont by the host can favor asexuality, or at least can allow asexual lineages to persist, in the face of Red Queen challenges. In the coevolutionary race between banana's human symbionts and its pathogens, increasingly sophisticated intervention may be necessary to save the crop from extinction (Pearce 2003).

3

Domesticated plants as models in evolutionary ecology

We argue that integrating ecology – and in particular that of clonally propagated crops – into domestication studies can lead to fundamentally new insights. To a degree, each clonally propagated crop has its own domestication syndrome. These plants can thus provide model systems for studying a different, and collectively much larger, set of ecologically important traits than the seed-propagated crops on which most evolutionary research has focused so far (Doebley 2004,

Ross-Ibarra *et al.* 2007). The three crops presented in this chapter include only a small fraction of the plants, structures, and characters that have evolved under domestication, but they illustrate evolution in a great range of traits. They show the interest of these plants for studying the evolution of phenotypic plasticity and investigating the genetic basis of complex ontogenies. It is certain that in-depth study of a wider selection of crops would multiply the opportunities. The literature suggests that many other clonal crops have evolved under mixed clonal/sexual systems similar to those explored in the examples presented here. These include potato (Johns and Keen 1986), taro (Caillon *et al.* 2006), ensete (Shigeta 1996), and sweet potato (Yen 1974).

Seed-propagated crops and clonally propagated crops can thus each make unique and complementary contributions to evolutionary studies. Comparative studies of parallel and convergent evolution in cereals and grain legumes will continue to provide detailed information about the genetic and developmental basis of a few well-studied traits, whereas clonal crops, once we know enough about their ecology to intelligently use the genetic tools available for them, could provide good material for studying a host of other traits.

Clonally propagated crops could also add new twists to themes already explored in seed-propagated crops, such as the evolutionary role of gene flow between crops and wild relatives (Duputié *et al.* 2007). Crop–wild hybridization is often approached as a problem in managing the consequences of gene flow so as to conserve genetic resources and prevent the evolution of invasive weeds (Ellstrand *et al.* 1999), but its study can also give insights into fundamental questions about speciation (Ladizinsky 1998). Ecological speciation plays an important role in the generation of biodiversity, but “the threads connecting genes and selection are still few” (Schluter 2009). Crop plants and their wild relatives could provide model systems for studying links between adaptive divergence and reproductive isolation. Whether one approaches the problem from an applied or fundamental standpoint, a potentially important difference between seed-propagated and clonally propagated crops needs to be taken into account. In the former, selection pressures on seed dispersal and seed dormancy are strongly divergent between crops and their wild relatives. Depending on the environment(s) in which hybrids live, this could impose biological barriers to their viability at very early stages of ontogeny. Although these and other barriers to hybridization are far from impermeable, they act as a selective filter channelling introgression (e.g., Papa *et al.* 2005). In contrast, in clonally propagated crops, selection under domestication has not acted to reduce seed dispersal and dormancy. To the extent that volunteer plants from seed are important contributors to the crop’s genetic constitution, selection has acted instead to *maintain* traits essential to the plant’s sexual reproductive ecology, as in manioc and guinea yams. Crop–wild hybridization may thus face fewer biological barriers at crucial early stages of plant development than in many seed-propagated crops. However, the case of manioc shows that selection on volunteer plants from seed can lead to divergences in traits affecting sexual reproductive ecology (Pujol *et al.* 2005b), albeit very different from those involved in the classical “domestication syndrome.”

Their unusual reproductive systems could make clonal crops tractable models for exploring open questions about evolutionary dynamics in mixed clonal/sexual strategies (Halkett *et al.* 2005). Finally, those crops whose populations have undergone strictly clonal evolution for a long time, such as many bananas, could offer rare opportunities to examine genomic evolution in the absence of recombination (Judson and Normark 1996). For example, how rapidly do meiotic genes become nonfunctional (Schurko and Logsdon 2008)? Plants such as cardoon (*Cynara cardunculus* L., Asteraceae) could be particularly interesting models in this regard. Leafy cardoon and artichoke were both domesticated from the same wild ancestor, the former propagated from seed as an annual, the latter vegetatively as perennial clones (Sonnante *et al.* 2007). Comparative studies could give data on the effect of clonal propagation on genetic structure and genome evolution.

4 Ecology and crop improvement and management strategies today

Ecology must also make essential contributions to crop improvement today. Major challenges must be faced. What kinds of crop plants, and agroecosystems, can we devise that will ensure food security for growing populations while maintaining ecosystem services and biodiversity (Siedow 2001)? How can our crops and agricultural environments adapt to climate change (Smit and Skinner 2002)? A solid understanding of crop ecology is crucial to these endeavors. Domestication and “improvement” may have bred out traits that would be useful in tomorrow’s crop environments. Crop roots and their interactions with environment are a particularly neglected facet of the ecology of domestication. Waynes and Ehdaie (2007) point out that domestication over the past 10,000 years has largely proceeded with observation and direct selection of mostly aboveground organs, unless roots were used as food and selected for directly. Belowground organs, up to half of the plant or more, were neglected. For example, high yield in the “green revolution” dwarf wheats of the 1970s entailed not only the well-known reduction in aboveground vegetative parts, but also – as an unconsciously selected pleiotropic effect – the dwarfing of root systems as well. It should be possible to increase yield, particularly under future conditions of increased drought stress but even in irrigated/fertilized conditions, by selecting specifically for larger root systems. Similarly, plant breeding, largely targeting performance in nutrient-rich environments, has led to the reduced efficiency of root-symbiotic mutualisms (Kiers *et al.* 2007), which could be key allies of farmers in future environments. Another group of neglected friends are the wild relatives of crop plants, potential sources of many genes useful in agriculturally marginal environments (Heywood *et al.* 2007). But for wild relatives of many crops, unlocking their potential depends on better knowledge of their ecology, including their own response to climate change (Jarvis *et al.* 2008).

Responses to global change of farmers and of crops may both be complex, and their interactions even more so. As soils become degraded and droughts become

more frequent with climate change, farmers in some areas, e.g., southeastern Africa, shift from more demanding plants to manioc, because of its ability to yield even under marginal conditions. Insufficiently familiar with detoxification techniques, these new farmers of manioc are frequently affected by konzo and other diseases associated with chronic toxicity when this crop is improperly prepared (Nhassico *et al.* 2008). This problem could be aggravated by the plant's response to global change: under increased atmospheric CO₂ concentrations, manioc produces smaller roots with increased cyanogen content (Gleadow *et al.* 2008). Thus several factors may combine to produce a significant public health problem. Engineering cyanogens out of manioc is a frequently proposed solution (Siritunga and Sayre 2003), but it ignores the considerable evidence that the agronomic advantages of manioc in part result from its having a built-in pesticide (McKey and Beckerman 1993, Wilson and Dufour 2002). Such complexity shows that adapting crops and their environments to climate change will require all our ingenuity.

Notes

- 1 Evolutionary biologists avoid referring to any extant taxon as an “ancestor” of another extant taxon, preferring formulations such as “closest wild relative”. However, the recency of crop domestication makes it often possible to identify the wild ancestral taxon or taxa (if not the common ancestral populations), justifying our use of the shortcut term “wild ancestor” here.
- 2 February 2009, Jean Kennedy, Department of Archaeology and Natural History, Research School of Pacific and Asian Studies, Australian National University.

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18 Agrobiodiversity Shifts on Three Continents Since Vavilov and Harlan: Assessing Causes, Processes, and Implications for Food Security

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If we consider the “life cycle” of a domesticated species, we might divide it into six phases: (1) wild harvesting and (potentially) disruptive selection; (2) incipient cultivation and adaptation to agro-habitats; (3) domestication through cultural selection of a limited gene pool in agro-habitats; (4) diffusion and adaptation to other agro-habitats, with potential introgression with wild or domesticated relatives; (5) diversification and further selection through intentional breeding or fortuitous introgression; and (6) local extirpation and in some cases, global extinction. Although science historians primarily regard Nikolai Vavilov and Jack Harlan in terms of their contributions to our understanding of crop domestication and diffusion (Nabhan 2009), they were actually intellectually and practically engaged to some extent in observing and reporting on all six of the phases noted above.

Since the deaths of Vavilov and Harlan, there has been tremendous progress made in our scientific understanding of the first five phases in these crop life cycles, thanks to innovative collaborations among geneticists, archaeologists, biogeographers, ethnobiologists, and agricultural historians. However, one might argue that our scientific understanding of crop extirpation and extinction processes has lagged far behind that which conservation biologists have gained for wild species. While the body of scholarly literature on agricultural origins and dispersals has grown exponentially since the pioneering work of Vavilov, Sauer, Harlan, deWet, Zhukovsky, Zohary, and Darlington, we have largely seen anecdotal evidence and emotive interpretations regarding the causes, cultural processes, and consequences of genetic erosion, local crop extirpations, and global extinctions. There are exceptions, of course, such as the fine work of Stephen Brush, his colleagues, and students, but these notable exceptions prove the rule.

Perhaps this apparent lacuna is because the process of genetic erosion, first speculated about in correspondence between Nikolai Vavilov and Harry Harlan,

but fully articulated by Frankel (1970), has been more difficult to document than initially imagined. This may be due to the fact that “time-series data are not generally available for crops or agriculture in centers of diversity, and different or even incompatible measures of biological variability are used at different times” (Brush 2004: 160). Agricultural historians have often lacked detailed (varietal-level) inventories from which one can determine whether traditional crop landraces have indeed been conserved over considerable time *in situ*, or have suffered (undetected) turnovers, leading to genetic erosion through time. In particular, there is inadequate documentation of what Duvick and Worede term “evolutionary conservation”. This is the process whereby crop varieties maintained *in situ* continue to evolve through time to changing conditions such as increasing soil salinity or to dynamic interactions with crop pests (Worede 1997).

Nevertheless, there are untapped field notes, historic photos, archaeological data, and “gray literature” that have the potential to be better used to assemble such time-series on shifts in agrobiodiversity. While many agricultural historians laud Vavilov’s and Harlan’s contributions to *ex situ* conservation of plant genetic resources, less use has been made of their crop inventories and agro-ecological notes on the *in situ* persistence of these same crop varieties. That is ironic, since in recent years, many have argued that the best means to dynamically conserve these plant resources is through *in situ* methods that return benefits to the original stewards of these resources (Altieri and Merrick 1987, Nabhan 1989, Worede 1997, Qualset *et al.* 1997, Worede *et al.* 2001).

One recurring problem in assessing the causes and degree of change in agrobiodiversity through time has been the general paucity of data taken at the initiation of a crop’s presence in a region, or at the very least, before changes began to accelerate: “Data on pre-modern crop populations are rare because the questions posed by genetic erosion arose after these populations had been affected by technological change” (Brush 2004: 160).

Moreover, genetic erosion is not the only shift that may occur in the crop inventory of a particular culture or landscape; that is to say, we can hypothesize several different kinds of shifts in agrobiodiversity that may be tracked in a rural landscape through time:

1. Alpha diversity of crop varieties (landraces) and species may increase due to local selection, introgression, and introduction from sources beyond the immediate landscape.
2. Alpha diversity may remain roughly the same, but compositional shifts may occur, as certain varieties may change their distributions in time, space (latitude and longitude), or elevation.
3. Alpha diversity may dramatically decrease (as it does in the classical definition of genetic erosion), or it may stay roughly the same while a few highly commercial varieties dominate production in the landscape and other varieties with lower market value become marginalized.

4. The entire inventory of traditional crops may be replaced by an altogether different inventory of (hybrid or GMO) crops as the overall rural landscape is restructured to support irrigated, mechanized crop production for livestock feeding, industrial processing, or export.
5. The entire rural landscape may be replaced by urban, suburban or exurban residential, resort, and industrial developments, by reservoirs, or by military zones in which little food is produced.

Of course, there are other possible scenarios as well, but all beg the same question: what ecological, cultural, geographic, or economic factors contribute to the tenacious persistence of historic crop varieties in one place, but allow them to disappear in another? In other words, why have some traditional agroecosystems remained biologically diverse and resilient, whereas others have become vulnerable, brittle, or depleted? Such patterns cannot be easily explained by merely referring to the stochastic processes which drive extinction processes of wild species according to the theory of island biogeography (MacArthur and Wilson 1967); we must also turn to the resilience theories of ecologists and anthropologists, the community participation and control theories of conservation sociologists, and the political ecology theories of environmental historians, applied anthropologists, and geographers.

In the following case studies, we will briefly highlight trends and other patterns in agrobiodiversity shifts over the last century, roughly since the time when Nikolai Vavilov, Harry Harlan, Robert Forbes, Homer Shantz, and other plant explorers accomplished the first benchmark studies of crop diversity in particular landscapes. We will then attempt to interpret the processes driving these shifts. Finally, in conclusion, we will speculate on their ultimate causes and consequences for our food security, if only to stimulate more scientific analysis and scholarly consideration of them.

1 Selection of landscapes and elaboration of time-series

Although plant explorers such as Vavilov and Harlan often took detailed field notes during their plant explorations, there is not always comparable data from either before or after their visits with which to compare their data. While one of us (GPN) has recently come upon data from the eighteenth century for the agricultural oases of Baja California with which one can compare contemporary data (Nabhan *et al.* 2010), in most cases such time-series can only be assembled for the last century of active scientific expeditions. Ideally, such time-series should include data from at least three time periods over the same century, to establish whether or not shifts are unidirectional, as implied (but not necessarily tested) by most commentaries on genetic erosion. The time-series should be assembled from discrete landscapes, and in particular, from farming villages of the same cultures and at the same elevations as sampled in the past. Crop inventories are best done

in the primary (or indigenous) language spoken in the landscape, assembled from five or more fields in the landscape, assisted by local farmers, agronomists, or botanists who can visually identify crops down to the varietal level. Linguistic as well as agronomic reports from the area should both be consulted to construct comparable ethno-taxonomies for crop inventories. At the same time, it should be remembered that an ethno-taxon is not necessarily equivalent to a genetically distinct crop variety as identified by microsatellite data used to construct cladistic diagrams of intraspecific crop diversity. Lacking historic genetic analyses comparable to what can be done today, we can only use ethno-taxa as surrogates for assessing the alpha diversity of crops in a landscape.

For the purposes of this discussion, we will focus on three agrarian landscapes for which we have been fortunate enough to assemble such time-series: the Western Pamiri Highlands of the Gorno-Badakhshan Autonomous Province of Tajikistan (which Vavilov first visited in 1916); the Siwa oasis of western Egypt (which Vavilov was restricted from visiting, even though a contemporary and acquaintance, Robert Forbes, was able to visit for several months in 1919); and the Hopi, Tewa, and Navajo mesas of northern Arizona, USA (which Vavilov and a Forbes colleague, Homer Shantz, visited in 1933). Details of the time-series constructions are elaborated by Nabhan (2007) for the Siwa oasis case study, and with a few exceptions that will be noted below, are elaborated in a similar manner by Nabhan, Aknazarov, and Kassam (in preparation) for the Pamirs, and by Nabhan, Johnson, and Kelly (in preparation) for the Hopi-Navajo-Tewa mesas.

2 Case Study 1: Western Pamiri highlands

The rugged and remote geographic region of the Western Pamiri highlands – “the Roof of the World” or *Bam-i-Dunya* in Farsi – has attracted many explorers across the ages, including Nikolai Ivanovich Vavilov. While Vavilov actively collected crop genetic resources on five continents, he held the cultivated flora of the Pamirs with such special regard that he visited the region three separate times, in 1916, 1924, and finally, in 1929 (Vavilov 1997). Calling it “a natural laboratory” for understanding crop evolution, Vavilov hypothesized that the cultivated flora of the Pamirs harbored such a unique set of crop resources because of the convergence of four factors.

1. Its rugged mountainous terrain that made each one of its river valleys geographically remote from the next, and provided refuges for evolutionary processes to occur in relative isolation. Aridity reinforces this isolation, since the average annual precipitation in the Pamiri valley is estimated to be roughly 263 mm/year, but in places, as little as 60 mm, enabling agriculture to be practiced only on small patches of irrigable land scattered across a vast and socially fragmented landscape.



Figure 18.1. Perched valleys in the Khuf tributary of the River Panj, within the Pamiri highlands of Tajikistan.

2. The wealth of wild relatives of crops in its native flora, and early arrival of agriculture to the region, such that there was ample opportunity over 8,500 years or more for genetic introgression between domesticated landraces and their wild congeners.
3. The relatively high base elevation of the Pamirs – more than 70% of the land lies 2,500 m above sea level – demands that farmers introduce and evaluate, then select and adapt landraces for early ripening in order to survive short growing seasons.
4. The biocultural and linguistic diversity of the Pamirs and adjacent Afghanistan, and their possible roles in selecting and “encoding” differences among distinctive crop landraces in the region. Vavilov was perhaps the first scholar to articulate in print a tangible relationship between biocultural diversity and agrobiodiversity.

This case study focuses on three watersheds of Western Pamirs of the Gorno-Badakhshan Autonomous Province that lie within 200 km of Khorog, as tributaries of the River Panj: the Shakh dara, Gunt, and Khuf (Figure 18.1). We have used crop inventories from farmers’ fields in the Rushani-, Shughni-, Ishkashemi-, and Wakhi-speaking valleys of the Pamirs that have been collected over a century’s time, beginning in the 1890s with S.I. Korzhinsky (Vavilov 1997: 5) and Olufsen (1904), building on Vavilov’s detailed notes from 1916, and including our own September 2006 surveys.

With regard to notes on the historic upper elevational limits of selected crops, we have used casual notes from the Panj taken by Olufsen (1904) between 1896

and 1899, and more formal ones from Korzhinsky (Vavilov 1997: 5), which Vavilov believed at the time to be on the average of 300 m too low compared to his observations in 1916. However, in his monograph on the cultivated flora of Gorno-Badakshan (Vavilov 1916), as well as in later works, Vavilov cites his own crop- or variety-specific elevational estimates that vary from this 300m variance from Korzhinsky's earlier estimates, that may either indicate changes since Korzhinsky's time, or differences in the accuracy of the methodologies they employed. In any case, we have used Vavilov's actual crop-specific record, rather than assuming that all crops shifted the 300 m average.

Our own estimates come from elevational ranges for villages where we accomplished crop inventories in four tributaries of the River Panj in August and September 2006, augmented by hand-held Garmin eTrex Vista global positioning system estimates taken by staff of the Pamir Biological Institute in autumn of 2006. In particular, our team sought out the highest known elevational limits of certain crops grown away from or between villages in these four valleys, the Gunt Darya, Shoh Darya, Khuf Darya, and Upper Pinj Darya east of Ishkashim. These data are to some extent corroborated or interpreted through 120 interviews in fourteen villages undertaken in Badakhshani areas of Tajikistan and adjacent Afghanistan by one of us, (K-AK) in July and August 2006.

Table 18.1 compiles various estimates of the upper limits of crop species distributions recorded in the Western Pamirs over the past 113 years. Because these data have been taken with different methodologies, and with various degrees of tight focus on specifically recording upper elevational limits, not all may be strictly comparable. Nevertheless, these preliminary results suggest that several crops (including wheat and barley) are now grown as least 610 m above where Korzhinsky or Olufsen reported them to be over a century ago, and that more recently introduced maize may now grow 1,520 m above where it was first reported.

Such shifts may be due to a combination of factors, including (1) introduction of cold-tolerant or earlier-ripening varieties from other regions; (2) further local adaptation of landraces for early ripening; and (3) responses to longer growing seasons due to global warming. Conditions certainly appear to exist for both possibilities (1) and (2). Farmers are continually anxious to increase the vertical range for their crops because of the shortages of arable land in the river valleys and the rapidity with which the season ends in September at 3,000m.

Badakhshani farmers are keenly aware of properties of different varieties and always anxious to experiment. While planting materials do not circulate freely in this society, varieties move across social networks within families and through marriage, as well as through trade and friendship. Meanwhile the expansion of the road networks across the region – even in Afghanistan – over the past century and the associated human and commercial mobility may well have expanded the potential for varietal exchange by linking more farming communities together. Although this was balanced for many years against the closure of the borders between Soviet Central Asia, China, and Afghanistan, the recent re-opening of

Table 18.1. Elevational shifts in crop distributions in the Western Pamirs, 1893 to 2006

			Upper elevational limit (m) ^a				
Scientific name	English	Tajik	A	B	C	Change	Note
<i>Triticum aestivum</i>	Wheat	Gandum	3,250	3,550	3,860	+610	Ancient
<i>Hordeum vulgare</i>	Barley	Djou	3,250	3,550	3,860	+610	Ancient
<i>Secale cereale</i>	Rye	Lashak	3,250	3,550	2,800	−350	Ancient
<i>Zea mays</i>	Maize	Jugoree	1,980	2,280	3,500	+1,520	Post-Czarist
<i>Eleusine coracana</i> or <i>Pennisetum</i> <i>miliaceum</i> and/or <i>Setaria italica</i>	Finger millet and Foxtail millet	Arzan Pinj	2,690	2,570	2,900	+300	Ancient, now declining or rare
<i>Avena sativa</i>	Oats			2,100			Ancient, now as weed only
<i>Linum usitatissimum</i>	Flax	Zigir			2,800		Ancient, now absent or rare
<i>Vicia faba</i>	Fava bean	Boklo	2,510 or 2,702, up to 3,029?	2,810	2,900	+400	Ancient
<i>Pisum sativum</i>	Pea	Garoch	3,250	3,850	2,900	−350	Ancient
<i>Lathyrus sativus</i>	Chickling vetch	Mash					Ancient
<i>Phaseolus coccineus</i>	Runner bean	Fasulya					Post-Soviet
<i>Cicer arietinum</i>	Chickpea	Nut			2,700		Ancient, now declining or rare
<i>Solanum tuberosum</i>	Potato	Chacho-lu, Kartoshka			3,200		Post-Czarist
<i>Cucurbita pepo</i>	Pumpkin	Cadoo Kilo	2,702 (or up to 3,029?)		3,200	+298/161	Post-Soviet
<i>Cucumis sativus</i>	Cucumber	Bodering			2,900		Post-Silk Road
<i>Brassica napus</i>	Rape/Turnip	Turp		2,500+	2,750	+250	Ancient, declining as oilseed
<i>Carthamus tinctorius</i>	Safflower	Saffloor			3,000		Post-Silk Road, now absent or declining
<i>Gossypium herbaceum</i>	Cotton	Pachta					Post-Czarist, now absent or declining
<i>Helianthus annuus</i>	Sunflower	Oftob Parast			2,750		Post-Soviet
<i>Helianthus tuberosus</i>	Sunchoke	Qalamfur Murch			2,800		Post-Soviet
<i>Medicago sativa</i>	Alfalfa/Lucerne	Unishka Gorj	2,702 ?		2,750	+48	Post-Soviet
<i>Melilotus alba</i>	Clover	Esparcet			3,200		Post-Soviet
<i>Citrullus lanatus</i>	Watermelon	Tarbuz	2,702 (or up to 3,029?)		2,600	−102/ +429	Post-Soviet
<i>Lycopersicon</i> <i>esculentum</i>	Tomato	Pomedor			3,020		Post-Soviet

Table 18.1. (cont.)

Scientific name	English	Tajik	Upper elevational limit (m) ^a				Note
			A	B	C	Change	
<i>Nicotiana tabacum</i>	Tobacco	Tabakh			3,000		Post-Soviet, increasing
<i>Nicotiana rustica</i>	Turkish tobacco	Tabakh	2,702 (or up to 3,029?)		2,900	+198	Post-Columbian, declining
<i>Cannabis indica</i>	Hemp, hashish		2,702 (or up to 3,029?)				Now absent or declining
<i>Morus nigra</i>	Mulberry	Tut	2,702 (or up to 3,029?)		2,700	–2	Post-Silk Road, declining
<i>Malus × domestica</i>	Apple	Seeb, Mun	2,702		3,000	+298	Ancient
<i>Pyrus communis</i>	Pear	Nokh	2,702		3,000	+298	Ancient
<i>Prunus armeniaca</i>	Apricot	Zardolu, Nosh	2,702 (or up to 3,029?)		2,900	+298	Ancient
<i>Prunus cerasus</i>	Cherry	Alicha			2,700		Ancient
<i>Prunus domestica</i>	Plum	Oleu, Sliva			3,000		Ancient
<i>Prunus persica</i>	Peach	Shatooly	2,150		2,700	+550	Ancient
<i>Vitis vinifera</i>	Grape	Amrud	below 2,200	2,000	2,600	+400	Ancient
<i>Juglans regia</i>	Walnut	Bojak, Chormagz	2,702 (up to 3,029?)		2,750	+48/–279	Post-Czarist
<i>Daucus carota</i>	Carrot	Sabzi			3,000		Post-Czarist
<i>Beta vulgaris</i>	Beet	Sharam-cha			2,900		Post-Czarist
<i>Allium cepa</i>	Onion	Pios			2,800		
<i>Allium sativum</i>	Garlic	Siir					
<i>Brassica oleracea</i>	Cabbage	Karam			3,000		Post-Czarist
<i>Capsicum annuum</i>	Chile pepper	Balgaski Peret			2,900		Post-Soviet
<i>Anethum graveolens</i>	Dill	Ookrob			2,850		Ancient
<i>Mentha piperata</i>	Mint	Pudina			3,000		Ancient
<i>Coriandrum sativum</i>	Coriander	Gashniz			2,900		Ancient
<i>Hypericum scabrum</i>	Thyme	Choykahaak or Zevarraboy			3,240		Post-Soviet
<i>Amaranthus cruentus</i>	Cock's comb amaranth	Tojik Kharus			2,750		Post-Soviet

Note:

^a See text for citations.

A: Observations by Korzhinsky in the year 1893 and Olufsen in the years 1896–9.

B: Observations by Vavilov in the year 1916.

C: Observations by Aknazarov, Nabhan, Monti in the year 2006.

these borders (including many bridges across the Panj in the past few years) has led to a flurry in crop varietal exchanges. It would not be at all surprising if one of the criteria sought in these exchanges was superior productivity at high altitude. Extended fieldwork tracing the history of landraces alongside social network analysis could establish the significance of this for the increased altitudinal tolerance of many crops in the region.

In summary, the case study from the Pamiri highlands appears consistent with the second hypothesis, where, to date, shifts in composition and elevational amplitude seem the prevailing dynamic, rather than genetic erosion (hypothesis 3) *per se*. If we remove from consideration the three examples for which there have been equivocal elevational shifts since the 1890s, our preliminary assessment suggests that 16 crop species have shifted upwards elevationally an average of 311 m between the 1890s and 2006; in addition, ten crop species have shifted an average of 315 m between 1916 and 2006.

This trend is not surprising, given that glaciers in the Pamirs have shrunk in size up to approximately 20% during the past 30 – 35 years, presumably as a result of global warming (Khromova *et al.* 2006). The dramatic climate changes that have occurred in the Pamirs since the 1960s are so remarkable that they have been meticulously monitored and modeled over several decades (Anonymous 2002). These studies suggest significant increases in winter and spring temperatures at higher altitudes, on the order of 0.1 – 0.7°C/yr. At the same time, an increase in cold air drainage down through the lower Pamir foothills into the flood-plain fields of irrigated valleys has resulted in a 0.1 – 0.3°C/yr decrease at some lower elevations (Anonymous 2002). These models suggest the possibility of warmer, longer growing seasons where agriculture is practiced at mid-to-high elevations, and cooler spring and summer seasons at lower elevations, especially where cold air drains and settles onto arable flood plains. However, some elevational shifts in crop ranges cannot be explained by warming trends alone; some grains, such as wheat, are being planted over a broader amplitude owing to cultural shifts in preferences for cereals to be used as breads and porridges. There is concern in many parts of the world that some fruit trees are now having difficulty obtaining their minimum requirement of “chill hours” needed to trigger the physiological development of floral buds, and later, fruit (e.g., Luedeling *et al.* 2009).

And yet, Badakhshani farmers are not passive victims of such consequences of climate change; some farmers are currently planting experimental “common gardens” of fruit and nut trees taken from other elevations to see which best fit current (and future?) conditions. In summary, our time-series data suggest the accelerating influences of climate change, as well as proactive responses by farmers to it. In particular, trends appear to include the relative diminution of barley, rye, and oats, as wheat expands upward; and the difficulties found in getting apricots, mulberries, and apples to bear fruit where they once yielded abundantly. Olufsen (1904) noted that apricots were the most important fruit crop in the Upper River Panj, and that mulberry fruit were commonly used for bread; Vavilov also noted the latter. One of us (K-A K) has interviewed a number of farmers who are now

having difficulty getting time-tried varieties of tree crops to bear fruits or nuts at the same elevation where they have typically produced for a century. As a result, the farmers are actively seeking other varieties to try from farmers at higher elevations or from other river valleys.

3 Case Study 2: Siwa Oasis of Egypt

As noted in Nabhan (2007), a unique opportunity to compile time-series data on crop inventories was enabled by a contemporary and acquaintance of Vavilov, Robert Forbes (Colley 1987). We were fortunate to have discovered a rather detailed site-specific crop inventory from Siwa oasis, which Forbes elaborated during a month-long stay there during September of 1919; his data are complemented by data from Belgrave (1924), from Fakhry (1973) during 1968 and 1969, and from the senior author's visits to Siwa during 2004 and 2006 (Nabhan 2008).

The oasis of Siwa is located 300 km south of the Mediterranean port town of Marsa Matruh, Egypt, in the 1,000 km² Siwan Depression that lies as much as 18 m below sea level on the northern edge of the Great Sand Sea of Egypt's Western Desert or Sahara (Vivian 2004). Of the 240,000 acre depression, some 9,200 acres are in crops irrigated by some 200 springs and wells of the more than 1,828 artesian springs and seeps geologically recorded there. These 200 springs and wells have the capacity to produce 20 million cubic meters of irrigation water per year. The human population of Siwa includes 5,000 Ta-siwat- (Berber-) speakers belonging to some eleven *qabila* clans or tribes, of the permanent residents in the depression. Other residents include Awlad Ali Bedouins and Nilotic Egyptians, who speak various dialects of Arabic. Exchange of vegetables and fruits has occurred on the edge of the Shali, or Old City, for centuries (Figure 18.2).

For centuries, this oasis community has been almost entirely supported by agricultural production that utilizes the fresh, mildly alkaline, or highly saline waters of the oasis (Forbes 1921a, b, Fakhry 1973, Vivian 2004). Over the past century or so, this production has included anywhere between 240,000 and 300,000 date palms, as well as 25,000 olive trees (White 1899, Vivian 2004). These crops have in turn supported anywhere between 3,000 and 8,000 Siwans from 1800 to 1950, with the current human population just surpassing 12,500 people, perhaps due to improved health care (Vivian 2004).

Although some Siwan Berbers claim that their ancestors survived on only dates and olives as their plant foods, and sheep, goats, and dogs as their animal foods (Vivian 2004), it is clear from historic accounts (Hoskins 1837, White 1899, Forbes 1921a, b) that Siwans have long had a diversified agricultural base. Recent connections to Egyptian cities by asphalt (bitumen) pavement have intensified the introduction of other crops and foodstuffs to Siwa, and accelerated the pumping of water to meet the needs of non-Siwans living or visiting at or near the oasis. The following summary highlights nearly a century of shifts in Siwan agrobiodiversity.



Figure 18.2. Overview of the ancient Shali and date groves at Siwa, Egypt.

Table 18.2 presents the results of the time-series comparison of crops recorded in Siwa over the past 85 years. In the final column, we have noted crops that we found in the markets (M), including 14 species which have not otherwise been recorded in Siwan date groves, fields, or gardens. We assumed that most of these are from horticultural production areas along the Nile – either fields or hothouses – and have become common foods in Siwa only since the road from Marsa Matruh was paved in 1986. We have observed in date groves, fields, and orchards some 27 crop species or subspecies that had been recorded by previous observers that continue to be grown in Siwa. In addition, eight crops recorded by earlier observers that we did not see under cultivation remain in the marketplace, and in most cases, are likely to still be grown in Siwa; it is probable that our landscape-scale (but seasonally limited) survey simply missed where they were being cultivated. The crops that we assume are still grown at Siwa (that we did not see in cultivation) are: almonds; snake melons; cantaloupes; watermelons; tobacco; parsnips; and broad beans (favas). If this assumption is correct, 33 crop species (and one additional subspecies) recorded over the last century persist as components of Siwan agrobiodiversity. In every case in which a particular landrace or folk variety was earlier recorded, those same varieties persist at Siwa today (see Discussion for more detail).

Eight crops are now cultivated in Siwa that were not recorded by earlier observers: apples; guavas; prickly pear; zucchini squash; lemongrass; basil; and luffa sponges. Two others, banana and sugar cane, were introduced, apparently disappeared for a while, then reappeared. Some of these have been in the

Table 18.2. Siwan agrobiodiversity shifts: crop varieties present or absent

Scientific name	English	Cairene Arabic	Ta-siwit (Eastern Berber)	Forbes in 1919 ^a	Belgrave in 1924 ^b	Fakhry in 1968–1969 ^c	Nabhan in 2004–2006 ^d
<i>Phoenix dactylifera</i>	Date	BalaH: amhat, sai'idi (siwi), frehi (feryhy), gzahali, izzawi, taktakt	Tiin: sai'idi, al- qe, l-izzawi, taktakt	X	X	X	XM
<i>Olea europa</i>	Olive	Zaytuun	Azumer bi-Siwi	X	X	X	XM
<i>Musa paradisiaca</i>	Banana	Mawz	al-Mawz		Already lost		XM
<i>Vitis vinifera</i>	Grape	'Inab	Tizren		X	X	XM
<i>Citrus aurantiifolia</i>	Lemon	Laymuun	Laymuun	X	X		XM
<i>Citrus reticulata</i>	Tangerine-orange	Burtu'aan	Burtgan bi-Siwi	X	Already lost?	X	XM
<i>Ficus carica</i>	Fig	Tiin	Imuuchan	X	X	X	XM
<i>Malus × domestica</i>	Apple	TuffaaH	TuffaaH		X		XM
<i>Punica granatum</i>	Pomegranate	Rummaan	al-Monen	X	X	X	XM
?	stone fruit	T-burquayn	Nbe'ukt bi-Siwi				XM
<i>Prunus armeniaca</i>	Apricot	Mishmash	Mishmish	X	X	X	XM
<i>Prunus persica</i>	Peach	Xoox	Xoox		X	X	X
<i>Prunus domestica</i>	Plum	Burquq	Burquq		X	X	X
<i>Mora nigra, M. alba</i>	Mulberry	Tuut	Tuut			X	X
<i>Pyrus communis</i>	Pear	Kummitra	Kummitra		X	X	
<i>Ceratonia siliqua</i>	Carob	al-Qarub	Ti-jarobiin			X	XM
<i>Prunus amygdalus</i>	Almond	Lawz	Lawz			X	M
<i>Mangifera indica</i>	Mango	Manga	Manga				M
<i>Psidium guajava</i>	Guava	Gawaffa	Juwaffa				XM
<i>Opuntia ficus-indica</i>	Prickly pear	Tiin shaukee	Imuuchan tidriwinn		X		X
<i>Hibiscus sabdariffa</i>	Hibiscus/book roselle	Karkadeeh	Karkadeeh	X			XM
<i>Fragaria × ananas</i>	Strawberry						M
<i>Saccharum officinale</i>	Sugar cane	Qasab	Laksab		Already lost		XM
<i>Corchorus olitorius</i>	Jew's mallow	Muluxiyya	al-Muyixiyaad	X		X	XM
<i>Ricinus communis</i>	Castor bean	–	–				X

continued

<i>Abelmoschus (Hibiscus) esculentus</i>	Okra	Bamya	Bamya	X		X	X
<i>Solanum melongena</i>	Eggplant	Bidingaan	Lubginga	X	X	X	X
<i>Capsicum annuum</i>	Chile pepper (cayenne type)	Filfil (afdar, xatta, ruumi)	al-Filfil bi-Siwi	X		X	XM
<i>Cucurbita pepo</i>	Summer squash (zucchini type)	Kuusa	Kuusa				XM
<i>Cucurbita moschata</i>	Winter pumpkin (big cheese type)	Qarr	Likdiwa	X		X	XM
<i>Portulaca oleracea</i>	Purslane	Rigla	Makhmakh	X	listed as water-cress?	X	XM
<i>Lycopersicon esculentum</i>	Tomato	Taamatim	al-Taamatim bi-Siwi	X		X	XM
<i>Cucumis melo</i> var. <i>flexuosus</i>	Snake melon/gherkin Cucumber	Xiyaar	al-Xiyaar	X	X	X	M
<i>Cucumis melo</i> var. <i>cantalupensis</i>	Cantaloupe	Kantalubb, shamaam	TabaaxtoH	X			M
<i>Citrullus lanatus</i>	Watermelon	Battix	DaHmiksa	X			M
<i>Brassica rapa</i>	Turnip	Lift	Lift				M
<i>Pastinaca sativa</i>	Parsnip			X		X	M
<i>Raphanus sativus</i>	Radish	Figl	Lifgl		X		M
<i>Lawsonia inermis</i>	Henna	Henna	al-Henni				XM
<i>Nicotiana tabacum</i>	Tobacco	Tabr	al-Tabr	X			M
<i>Allium porrum</i>	Leek	Xurrat	Xurrat				M
<i>Allium cepa</i>	Onion	Basl	al-Filau	X	X		XM
<i>Allium sativum</i>	Garlic	Toom	TazaaH, tazaaHrot	X	X		M
<i>Petroselinum crispum</i>	Parsley	Baqduunis	Baqduunis		X		M
<i>Coriandrum sativum</i>	Coriander	Kuzbara	Kuzbara				M
<i>Vicia faba</i>	Fava broad bean	Ful	Iiwaawen	X			M
<i>Phaseolus vulgaris</i>	Common bean	Fasulya (beeda)	Fasulya				M
<i>Phaseolus coccineus</i>	Runner bean	Fasulya xadra	Fasulya xadra				M
<i>Lens esculenta</i>	Lentil	‘Adas	Tiinifayn				M
<i>Pisum sativum</i>	Pea	Bisilla	Besella				M
<i>Zea mays</i>	Maize	Durra	Yarldin		Already lost		M

Table 18.2. (cont.)

Scientific name	English	Cairene Arabic	Ta-siwit (Eastern Berber)	Forbes in 1919 ^a	Belgrave in 1924 ^b	Fakhry in 1968–1969 ^c	Nabhan in 2004–2006 ^d
<i>Oryza sativa</i>	Rice				Already lost		M
<i>Eleusine indica</i>	Millet	–	–	X			
<i>Hordeum vulgare</i>	Barley	Shieir	Tamizwa	X			X
<i>Triticum aestivum</i> , <i>T. dicoccum</i>	Wheat (Emmer and/ or Bread)	QamH	–	X			X
<i>Medicago sativa</i>	Alfalfa/Lucerne	Barsiim Higaazi	Gazaar	X			XM
<i>Melilotus officinalis</i>	Yellow sweet clover	Barsiim	–				XM
<i>Cymbopogon citratus</i>	Lemongrass						X
<i>Lactuca sativa</i>	Romaine lettuce	Xass	al-Xass				M
<i>Brassica oleracea</i> var. <i>botrytis</i>	Cauliflower	Qarnabiit	–				M
<i>Brassica oleracea</i> var. <i>capitata</i>	Cabbage	Kurumb	Kurumb				M
<i>Mentha arvensis</i>	Mint	Neana'a	Neana'a bi-Siwi	X	X		XM
<i>Ocimum basilicum</i>	Basil	Krumb	RiHaan				X
<i>Solanum × tuberosum</i>	Potato	Batatas	Batatas				M
<i>Ipomoea batatas</i>	Sweet potato	Batatas	Batatas				
<i>Colocasia esculentum</i>	Taro root	Aaz ool	Aaz ool				M
<i>Luffa cylindrica</i>	Luffa	–	–				XM

Note:

^a Forbes 1921b; X indicates presence.

^b Belgrave 1924; X indicates presence.

^c Fakhry 1973; X indicates presence.

^d Nabhan 2007; X documents 2004–2006 cultivation in Siwan fields or gardens; M documents presence in commercial markets in Siwa, largely brought in from distant sources.

Mediterranean Basin for centuries, but historically restricted access to Siwa may have delayed their introduction there. Others, such as apples and guavas, may have been limited until recently by the availability of nursery stock suited to the peculiar environmental conditions of desert oases such as Siwa (Bircher and Bircher 2004). Rice was apparently introduced early in the twentieth century, but was abandoned for fear of the mosquitoes and malaria associated with its cultivation in standing water (Belgrave 1924, Fakhry 1973). The more settled Bedu living on the outskirts of Siwa now benefit from access to water and electricity in their homes, and have begun to grow luffa sponges, bananas, and some unidentified herbs in dooryard gardens. One tree crop in a Berber oasis-garden at Abou Shrouf remains unidentified; it is a stone fruit with a Berber name, and is perhaps a minor species of *Prunus* (Bircher and Bircher 2004).

It appears that until recently, certain components of Siwan agriculture – overstory perennials such as landraces of dates and olives – have little changed though time, whereas some second-tier fruit tree species have been recently added to the traditional guild of fruit species, and annual crops have more frequently come and gone through time. However, recent globalization pressures (resorts, greenhouse production of vegetables, industrial farming of Kalamata olives for oil export) have increased the amount of spring water pumped for nonsubsistence purposes, leading to intensified salinization of irrigated lands and abandonment/conversion of some fields to nonagricultural uses. In essence, local sheiks have lost control of irrigation management, and exacerbated salinization is like a time bomb waiting to go off. The impacts of intensified salinization on agrobiodiversity are not yet fully understood, but should be intensively monitored by both agricultural and social scientists interested in resilience.

The mere presence of the same crop species some 85 years after the first Siwan crop inventory does not necessarily indicate that traditional cultural means of *in situ* conservation have been effective and that little genetic erosion has occurred. However, both farmers and market vendors in the souks proudly pointed out a number of folk varieties that they label as *bi-Siwi* in their Berber dialect, or *biladi* in vernacular Arabic. These labels refer to locally adapted landraces that Siwans believe (a) to occur nowhere else in the world; (b) to tolerate saline soils and alkaline spring waters more than introduced varieties have; and (c) to provide essential ingredients to Siwan cuisine that give their prepared foods distinctive flavors and textures.

The many new foods that have barraged Siwa since it was connected to Egypt's modern transportation network globalized the Siwan diet even before it began to globalize Siwan agriculture. Under the extreme heat and low humidity of the Sahara, exacerbated by saline soils and highly mineralized irrigation water, few wide-adapted high-yielding varieties (HYVs) may survive and thrive at Siwa. Its locally adapted landraces may ultimately outperform the many HYVs that are now available to Siwans in Marsa Martouh, by mail, and by internet, even under more salinized conditions.

In summary, the Siwan case study is complex, and can only be explained by hypotheses 1, 3, 4, and 5. However, the recent loss of local control over water management, and the recent investment in commercializing crops for export by Europeans, Canadians, and Americans may trump all other factors in the future. The political ecology of Siwa – particularly the influence of external (globalizing) pressures – deserves scrutiny.

4 Case Study 3: Hopi-Navajo-Tewa lands on the Colorado Plateau, USA

When Nikolai Vavilov visited the Colorado Plateau of the southwest USA with University of Arizona President Homer Shantz in 1932, he was witnessing some of the last resilient indigenous farming systems in the deserts of North America. At the height of the Great Depression and in the midst of the infamous Dust Bowl, Hopi, Navajo, and Tewa Indian farmers were not only providing over 95% of the foods required by their families; they were also exporting fruits, vegetables, grains, and other food products to surrounding Native, Anglo-, and Hispanic-American communities (Nabhan 2009). This was quite a remarkable feat, given that their farms occur in a sandy landscape that typically receives only 200 – 250 mm of precipitation per year, and during the Dust Bowl, when subaverage rainfall conditions prevailed. Although most Navajo, Hopi, and Tewa dry-farm their fields of grains, legumes, and certain vegetables, many also rely on spring-fed terrace gardens for intensified vegetable production between 1,400 and 1,600 m in elevation.

Although Vavilov and Shantz spent less than four days in the fall of 1932 among Hopi, Navajo, and Tewa farmers on the Colorado Plateau, their brief visit inspired others to immediately undertake more detailed surveys of Hopi crop varieties and their role in providing food security. Within two years, ethnobotanists Alfred Whiting and Volney Jones had collaborated with bilingual Hopi farmers to interview dozens of families with regard to the inventories of crops they grew; at nearly the same time, the USDA Soil Conservation Service undertook household surveys of food production and consumption among the Hopi, Navajo, and Tewa that complement the Jones-Whiting survey of agrobiodiversity. Until his death, Whiting continued to update his notes on the status of Hopi crops in the field; after he offered one of us (GPN) those notes, he collaborated with anthropologists Daniela Soleri and David Cleveland on a resurvey of Hopi crops using comparable methodologies in 1989, and formally approved by the Hopi Cultural Preservation Office. Soleri and Cleveland (1993) published only part of these data, which prompted the lead author to enlist the help of Shawn Kelly and Ferrel Sekacucu in initiating another resurvey in 2005. This resurvey was done with the kind assistance of farmers participating in the Natwani Coalition, which seeks to revive Hopi agriculture for many purposes, including local food security, tribal food sovereignty, and cultural/ceremonial obligations.

Cumulatively, the Hopi have grown at least 75 varieties of fruit, nut, vegetable, legume, and grain crops over the past century, but it appears that 45 of these were no longer being cultivated on any substantive scale by 2005. In short, 59% of the Hopi-named ethno-taxa or traditional crop varieties recorded by Vavilov, Shantz, Whiting, Jones, and others early in the twentieth century were no longer regularly cultivated at the end of that century, when another major drought devastated food production on the Colorado Plateau for seven years.

These losses did not all occur at the same time. Between 1895 and 1935, only four varieties appear to have been lost, accounting for only 8% of the total genetic erosion that occurred through 2005. Immediately after Vavilov's visit, from 1935 to 1989, 13 varieties were lost, amounting to 17% of the total genetic erosion that occurred through 2005. However, from 1989 to 2005 – a period marked not only by climatological drought but by depletion of Hopi springs by industrial over-pumping of the aquifer – 28 varieties appear to have been lost, amounting to 62% of the genetic erosion over the 110-year period. Particularly hard hit were landraces of gourds, common beans (replaced in the diet by government surplus pinto beans), and landraces of minor vegetable crops such as amaranths, Jerusalem artichokes, chile peppers, etc.

While water problems have certainly contributed to agrobiodiversity losses and shifts on the mesas of the Colorado Plateau as they have at Siwa oasis, the effects of globalization have also shifted Hopi, Tewa, and Navajo livelihoods away from farming to government work, educational work, and arts and crafts. Hopi agrobiodiversity shifts can be largely explained by hypothesis 3 – the classic explanation of genetic erosion. Notably, there has not been one-to-one replacement of traditional landraces by high-yielding cultivars. A modified hypothesis 5 – that an agrarian landscape where farming was the main livelihood has been replaced by an exurban landscape where fewer families farm – seems viable. Hopi, Navajo, and Tewa food security appears to have been severely compromised since World War II. Fortunately, Hopi tribal government programs as well as the grassroots Natwani Coalition and Black Mesa Trust are attempting to reverse these trends.

5 Conclusions

The pronounced differences in agrobiodiversity shifts on three continents – in Central Asia, North Africa, and Southwestern North America – remind us that farmers adopt and abandon crop varieties for a variety of reasons. Genetic erosion – a unilateral loss across the board – is not the only story to be told by time-series assessments of agrobiodiversity shifts. The issues of causes and consequences are even more complex, given that both local and global factors influence the political ecology of *in situ* conservation of agrobiodiversity. To date, agricultural scientists and ethnographers have focused largely on detailing the local dynamics, while anthropologists, environmental historians, geographers,

and political scientists have focused on what ecologist Dan Janzen (1986) calls the eternal external threats. It is time to use political ecological theory and new methods in crop genetic diversity assessment to come up with an integrative model of how to assess agrobiodiversity shifts and their causes and consequences through time and space.

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19 Indigenous Peoples Conserving, Managing, and Creating Biodiversity

Jan Salick

There is a constant barrage of information about people destroying “nature”. Just as an example, to quote from the National Science Foundation (emphases added):

Studies in Europe have drawn from 10,000 years of human occupation to illuminate human and environmental causes for increased **erosion** and **desertification** of the northern Mediterranean region. (NSB 99–133 1999).

And

...to better understand the human dimensions of **deforestation**... an interdisciplinary team... has combined theories of human decision-making about land cover conditions with detailed analyses of field sites. (NSB 00–22 2000)

We need to counter such statements with examples of people who act successfully as conservationists, managers, and creators of biodiversity. These could help us learn to solve many of the environmental problems we face and the issues we address (Fenstad *et al.* 2002). To quote but one counter-example:

[Amazon] ecoregions are highly dependent on the successful protection and possible expansion of a few indigenous reserves. (Soares-Filho *et al.* 2006)

This is not to advocate the “noble savage” (Dryden 1672) nor to say that indigenous or traditional peoples *always* conserve and manage natural resources, but there is much to learn from successful traditional methods and results in conserving and managing biodiversity (e.g., Redford and Padoch 1992).

The examples in this paper are from my own ethnobotany research in the upper Peruvian Amazon and in Tibet, but equally there are a myriad of ethnobiologists who have documented traditional management of biodiversity around the world, a smattering of whom I cite. The Yanesha and Tibetans are obviously dramatically different peoples and cultures in radically dissimilar environments, which nonetheless similarly value and use biodiversity to feed, clothe, and medicate themselves. Furthermore, both groups have much to teach about conservation of biodiversity. Here, this information is presented across incremental scales of

biodiversity: from genetic diversity, through species diversity (α diversity) and habitat diversity (β diversity), to landscape (γ diversity), and then temporal diversity (diversity over time). Finally, the effects of climate change on biodiversity and its conservation will be addressed, as well as how traditional peoples perceive, adapt to, and mitigate climate change. Further literature will be cited to support these examples.

1 The peoples, places, and cultures

1.1 Yaneshá

At the headwaters of the Amazon basin in central Peru, only a few hundred meters above sea level, the Yaneshá are an indigenous group who have hunted, gathered, and farmed sustainably for millennia (Salick 1989). Although they, like all people, adapt to the contemporary world, they do carry traditional knowledge about one of the most diverse tropical rainforests in the world. Their culture is typically Amazonian, with minimal material culture and nominal ceremony. Nonetheless, their traditional knowledge is profound and teaches us much about the complexity and conservation of biodiversity.

1.2 Tibetans

At the eastern end of the Himalayas, on the border of Tibet with China, sacred Mt Khawa Karpo rises 6,740m and traditional Tibetan villages cling to mountain sides or nestle in elbows of the upper Mekong River, dating back hundreds if not thousands of years. Tibetans farm high-elevation crops, herd animals including yaks, and collect traditional Tibetan medicines, food (especially mushrooms), and firewood from a huge elevational range of habitats. In the face of Chinese influx, they tenaciously conserve their culture, customs, and beliefs. Their traditional knowledge, which emphasizes adaptation and biodiversity, is put to the test now with climate change on a scale and speed never before experienced. Nonetheless, Tibetans perceive, adapt to, and mitigate climate change in ways that can teach us a great deal.

1.3 Genetic diversity

Through the processes of domestication – although we often speak about genetic bottlenecks – people often *increase* the genetic diversity of traits either not under selection or for which people select variation and diversity. In my work on cocona, *Solanum sessiliflorum* (Figure 19.1, Salick 1992a), tremendous diversity of fruit size and shape has been created beyond the small wild fruits. The Yaneshá actively select for this genetic diversity, collecting oddly sized and shaped fruits, which breed true because of maternal inheritance. Maternal inheritance is a form of non-Mendelian inheritance, most often caused by cytoplasmic inheritance.

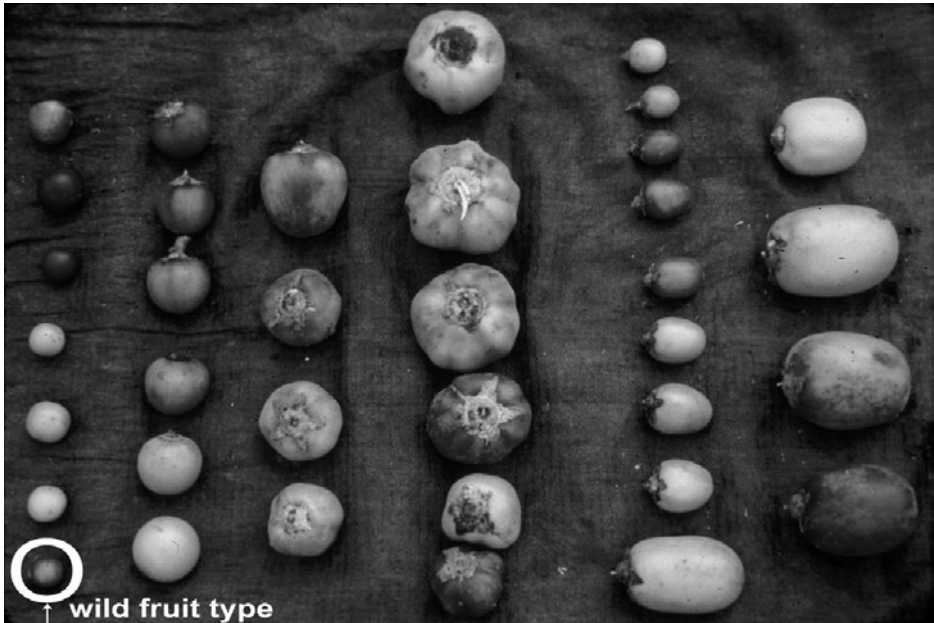


Figure 19.1. Diversity of cocona (*Solanum sessiliflorum*) fruit size and shape has been created by selection for novel fruit types by Yanesha and other indigenous peoples of the upper Amazon (from Salick 1992a).

In the case of cocona, fruit produced by seed plants (sexual offspring) look like fruits of the mother plant, regardless of the pollen donor. This maternal inheritance is selected because, when people plant seeds, they appreciate knowing what they will harvest. Thus, during domestication, in addition to people selecting for biodiversity and morphological and physiological traits, this study reminds us that people may also select for fundamental traits such as mode of inheritance.

Similar increases of diversity with domestication have been shown for many, many crops including the tomato as described by Charles Rick (1978) whose pioneering research at the University of California, Davis, was among the work honored by the holding of the 2008 Harlan Symposium in Davis, California.

2 Species diversity (α diversity)

Species richness and diversity characterize indigenous agricultural and forestry management and function to protect against risk (e.g., Carroll *et al.* 1990). If pests, disease, or weather destroy one crop (one species) there is always another substitute. Crop diversity also protects against pests and disease by damping pest population explosions and spread (Altieri and Nicholls 2004). The Yanesha plant more than 75 species of crop in home gardens (Figure 19.2a) and more than 125 species in swidden fields (Figure 19.2b and Salick 1989, Salick 1990, Hamlin and Salick 2003). This vast agrobiodiversity includes species rarely grown in

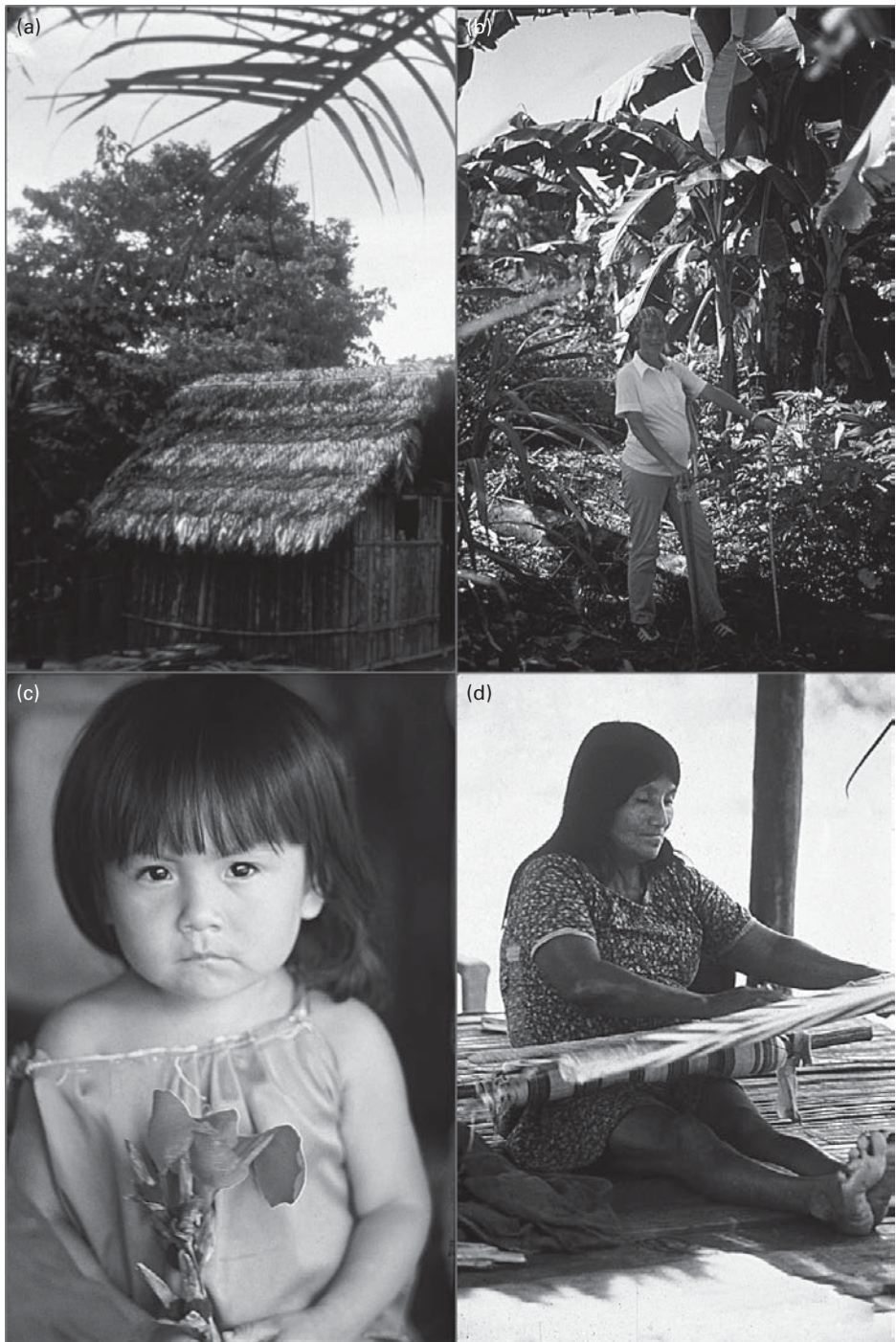


Figure 19.2. Species diversity in Yanesha agriculture: (a) Over 75 species in home gardens. (b) Over 125 species in swidden fields, including species rarely grown in nonindigenous agriculture such as (c) edible roots of the canna lily and (d) colored cotton used in traditional weaving.

non-indigenous agriculture, such as edible roots of the canna lily (Figure 19.2c) and colored cotton used in traditional weaving (Figure 19.2d). Many other studies on traditional agrobiodiversity come to the same conclusion (e.g., Ezyaguirre and Linares 2004) that species diversity in indigenous agriculture is unparalleled in other forms of modern agriculture. And yet, the tropical rainforest that the Yanesha actively manage (Salick 1992b) is an order of magnitude more diverse. This immense managed forest biodiversity is corroborated by many other scientists studying traditional forest management (e.g., Anderson 1990). In contrast, modern, western forestry most often simplifies forest composition and reduces natural diversity rather than augmenting it.

3 Habitat diversity (β diversity)

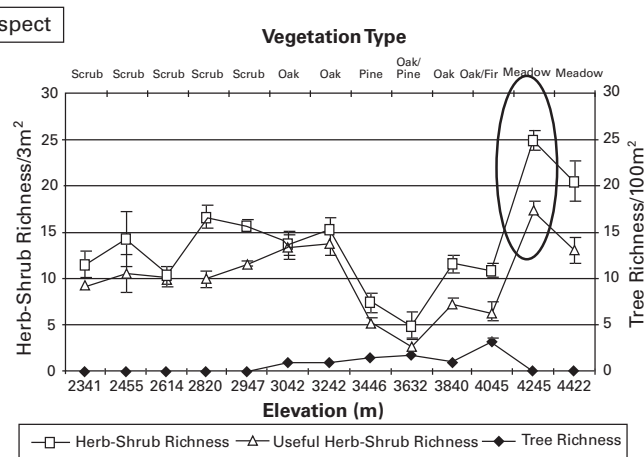
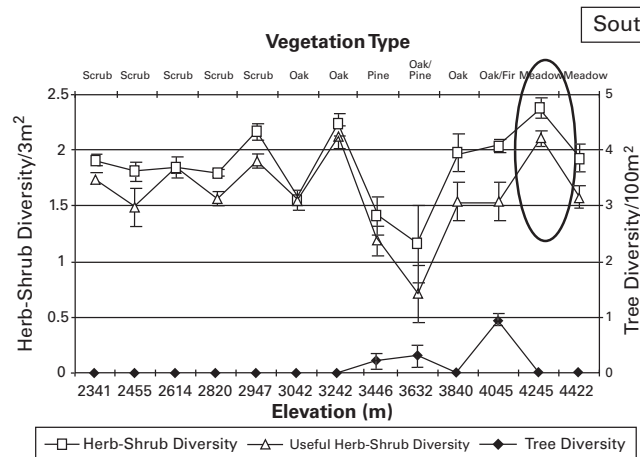
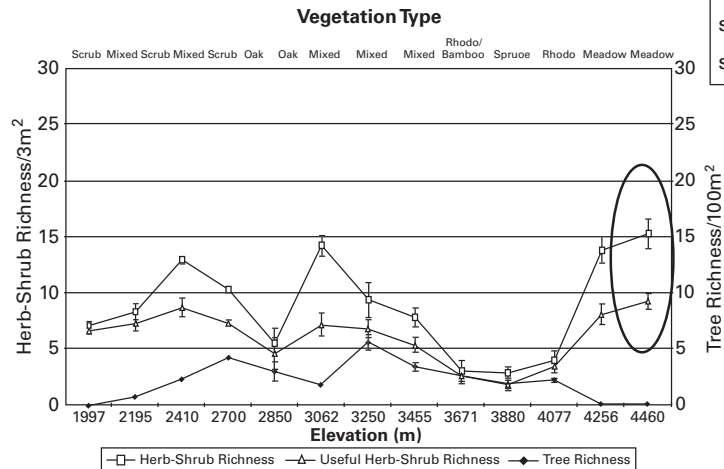
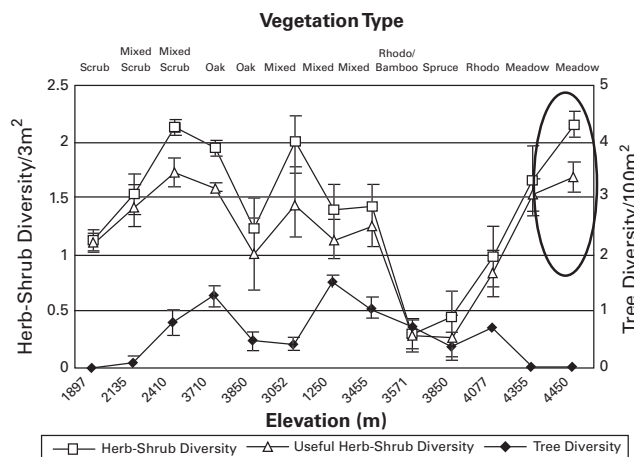
Diversity is not found at just one place at one time, but also among sites and over time. When considering diversity among sites we measure habitat diversity. This was a major focus of elevational gradient analyses that we conducted at Mt Khawa Karpo on the Tibetan border (Figure 19.3a and Salick *et al.* 2004). Starting at the Mekong River at about 2,000m elevation, we sampled vegetation every 200m vertical rise (Figure 19.3b, sampling 5 randomly located 100m² plots). Plant species, richness, and diversity varied among habitats, resulting in tremendously high

(a)



Figure 19.3. (a) At Mt Khawa Karpo on the Tibetan border, gradient analysis extended from 2,000m in the Mekong River valley (lowest point in picture) to the snow line at 5,000m.

(b)

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Northern Aspect

Caption for Figure 19.3. (cont.) (b) Richness and diversity (H') of herb-shrubs, useful plants, and trees over an elevational gradient from 2,000m to 5,000m (from Salick *et al.* 2004). Top: Southern aspect diversity (left) and richness (right). Bottom: Northern aspect diversity (left) and richness (right). Elevation and vegetation type at each site are given on the horizontal axes. Note that herb-shrub statistics are per 3m² while tree statistics are per 100m². Whiskers denote standard error (SE). Highest richness and diversity are found in Alpine meadows (circled).

habitat diversity. Tibetans use plants in all habitats for food, medicine, forage, fodder, fiber, dyes, and many other purposes. The most diverse habitat is the alpine meadows, where Tibetan doctors collect medicines and yaks graze in summer. However, no one habitat provides all plants for Tibetan livelihoods; Tibetans depend on habitat diversity. Similarly, in the Southwest US, Nabhan *et al.* (1982) showed how traditional subsistence and land use augments habitat diversity.

4 Landscape diversity (γ diversity)

However, Tibetan doctors collaborating with us were adamant about interpreting our data, *not* in terms of which habitat is most diverse nor even in terms of a gradient. Tibetan doctors and villagers insisted that we convey the fact that the entire landscape provides for their livelihoods (Salick *et al.* 2004, 2005). Tibetans are particularly well endowed with landscape diversity because of the elevational gradient, edaphic diversity, and microclimates, which make their varied livelihood strategies possible. In our technologically buffered western lives we often forget how important landscape diversity is in providing for cultural and livelihood diversities. Similar importance of traditional landscape diversity in Japan is well documented by Kobori and Primack (2003).

5 Diversity over time

Plant diversity can be measured and used not only over space, but also over time. Temporal diversity, like spatial diversity, exists at many scales. Among the Yanesha we measured changes in genetic diversity over time and successional diversity in agriculture, as well as succession in tropical rainforest diversity over time.

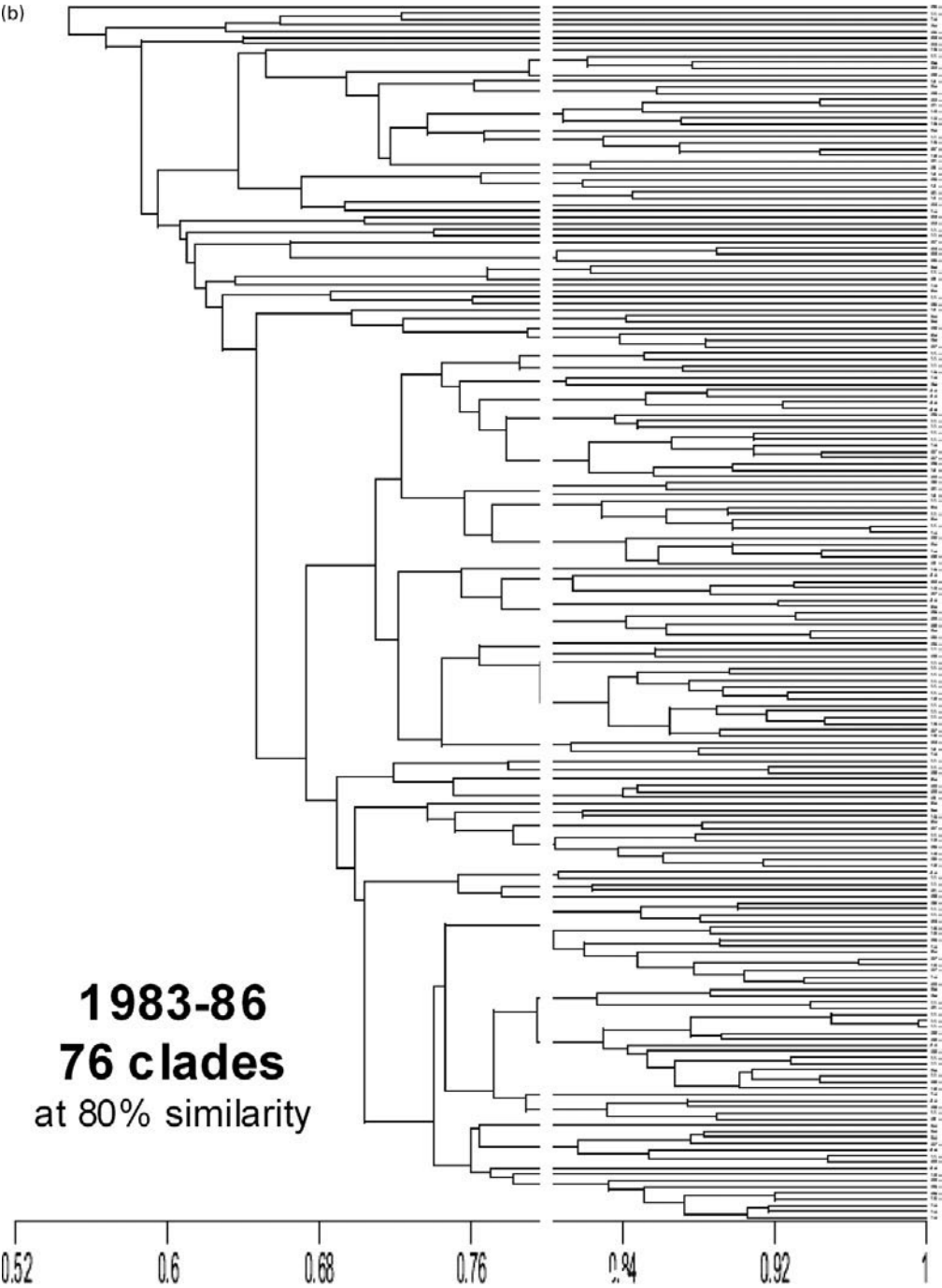
The staple crop for the Yanesha and most Amazonian indigenous peoples is cassava, *Manihot esculenta*. We systematically collected cassava cultivars among the Yanesha in the Palcazu and Oxapampa Valleys twice over a 15-year time period (Figure 19.4a): during 1983 to 1986 (Salick *et al.* 1997) and in 1999 (Salick *et al.* 2000). Over 200 cultivars were sampled from the same Yanesha families in 16 indigenous communities at both times, adjusting for aging families and deaths by adding new young families in 1999. Through cladistic analysis of morphological characteristics we determined that there were 76 cultivars in 1986 and only 66 cultivars in 1999 (assuming that plants 80% similar are the same cultivar) (Figure 19.4b and c). However, this loss of genetic diversity over time was not the surprising result. In 1999 there were only 8 of the 76 cultivars still existing from 1986! There had been a 90% turnover of cultivars in less than 15 years, representing tremendous diversity over time. This turnover can be explained by the accumulation of diseases in clonally reproduced crops, which forces people to constantly breed new cultivars. We had documented active indigenous breeding of cassava (Salick *et al.* 1997) and then documented the effect of this breeding

(Salick *et al.* 2000). McKey and collaborators (McKey *et al.* 2010 and his preceding publications) also document indigenous breeding of cassava.

Yanesha agriculture also shows habitat and landscape diversity over time (Figure 19.5). A swidden field goes through a succession of multi-crops over time (Salick 1989). For example, a lowland field is first planted with corn and beans (and a multitude of other crops); after six months cassava (and a multitude of other crops) is planted underneath, gaining dominance as the corn is harvested; after another year, bananas and plantains (and a multitude of other crops) are planted underneath, gaining dominance as the cassava is harvested; after another year, fruit trees are planted underneath, gaining dominance as banana and plantain production slows; and finally a managed fallow takes over, with a few patchy crops remaining until the cycle is resumed after a few years. This sort of



Figure 19.4. (a) Cassava varieties of the same Yanesha were systematically sampled in 1983–86 and in 1999, 15 years later. Here, the same woman is photographed in her cassava field during the first survey (inset photo) and second survey (larger outer photo).



Caption for Figure 19.4. (*cont.*) (b) Cladistic analyses of morphological characteristics of cassava varieties in 1983–6. Defining cultivars as those clades with 80% morphological similarity, there were 76 clades in 1983–86 and 66 clades in 1999 (see next page), indicating a substantial loss of genetic diversity over 15 years.



Caption for Figure 19.4. (cont.) (c) Cladistic analyses of morphological characteristics of cassava varieties in 1999. The singular result from comparing these data sets was that only 8 clades or 10% remained over time, indicating a huge turnover in cultivars in fifteen years and representing enormous biodiversity over time. Clonal crops need to be rotated in order to retain pest and disease resistance.

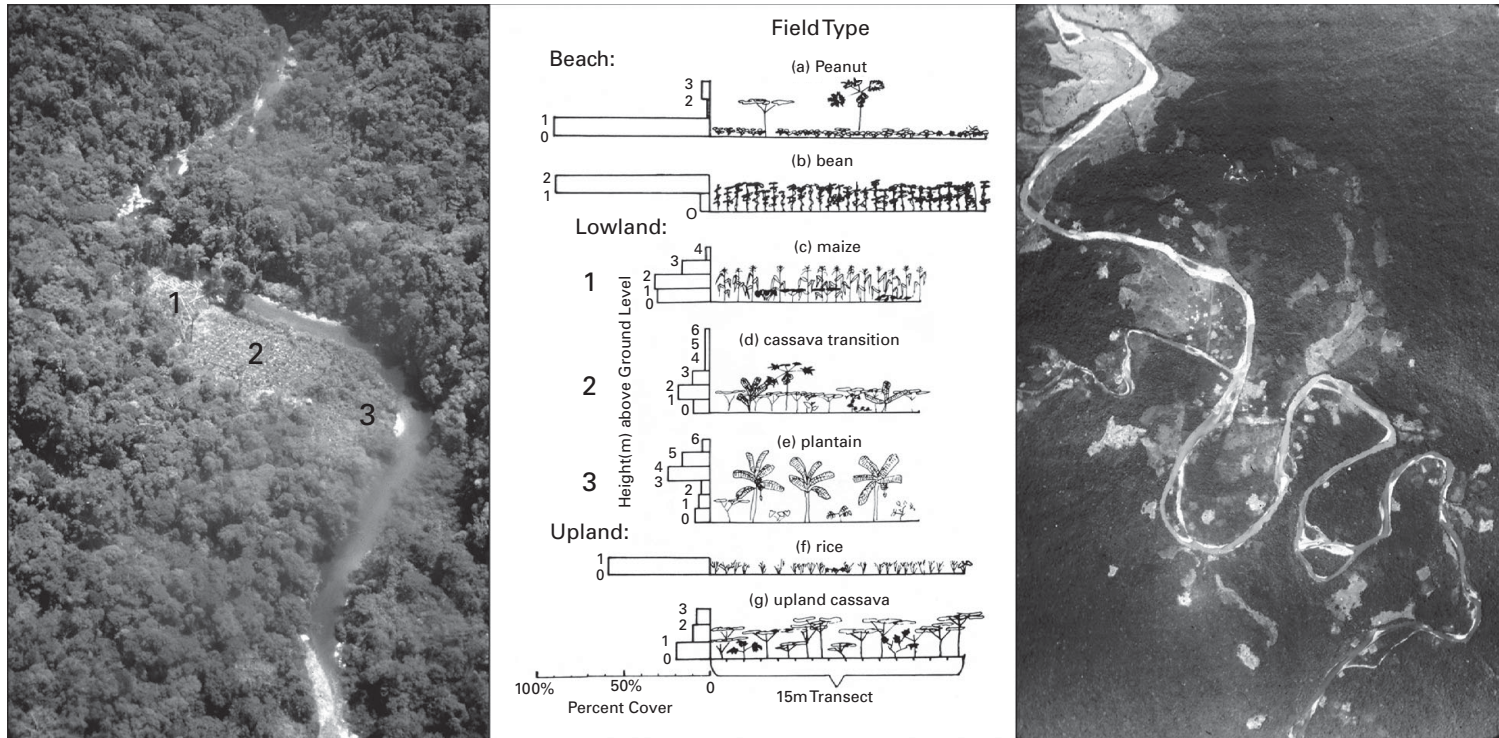


Figure 19.5. Yanesha agricultural diversity over time: habitat (left) and landscape (right) diversities. Three lowland agricultural fields (left) are at three different agricultural successional stages (center): (1) corn, beans, and minor crops, (2) cassava and minor crops, and (3) bananas, plantains, and minor crops. Different habitats (beaches, lowlands, and uplands) each have different agricultural successional stages (center), resulting in a very diverse, patchy landscape (right), constantly changing over time.

agricultural succession differs with habitat, so that the landscape diversity is a patchwork of different fields, at different agricultural successional stages including fallows. This patchwork varies over time producing a complex landscape with additional temporal diversity. Biodiverse succession in traditional agriculture including complex landscapes has been shown for a number of cultures around the world (e.g., Denevan *et al.* 1984, Uhl 1987).

6 Tropical forest management

It is noteworthy that although many of these examples are agricultural, forestry too plays a major role in indigenous natural resource management. The Yanéscha create, manage, and conserve tropical forest biodiversity by in-planting species, weeding undesirable species, releasing preferred species, killing pests, harvesting, planting seed, selecting, and by many more conscious, unconscious and often seemingly innocuous interventions (Salick 1992b). Tropical forest diversity increases with intermediate human disturbance (Salick *et al.* 1995) like the patchwork landscape pattern shown on the right in Figure 19.5 embedded within a matrix of tropical rainforest. Indigenous management of tropical rainforests can increase biodiversity in the same way that indigenous agriculture creates, manages, and conserves biodiversity (also see Posey 1985).

7 Climate change, biodiversity, and indigenous peoples

Indigenous peoples often find themselves on the forefront of climate change, directly faced with melting polar icecaps, desertification, inundated islands, or rapid Alpine change (Salick and Byg 2007, Salick and Ross 2009a,b). Mountains and their glaciers are often said to be “thermometers” of global warming (e.g., the documentary *An Inconvenient Truth* with Al Gore by Guggenheim 2006) because of their frozen history and rapid responses to climate change (Huber 2005, Nagy and Grabherr 2009).

After the polar regions, alpine environments are among those most affected by global climate change (Kullman 2004, Parmesan 2006, Nogués-Bravo *et al.* 2007, Salick and Byg 2007, Salick *et al.* 2009). Mountain ranges, where large numbers of endemic plants are distributed, are very likely to suffer critical species losses (Grabherr *et al.* 1994, 1995, Pauli *et al.* 2001, 2003, Theurillat and Guisan 2001, Halloy and Mark 2003, Pickering and Armstrong 2003). Alpine plant diversity is higher than the global average (Körner 1999, Väre *et al.* 2003). Indeed, our own studies in the Himalayas (Figure 19.3 above and Salick *et al.* 2004, Anderson *et al.* 2005) confirm that the highest plant diversity, richness, and endemism are found in alpine environments between 4,200 and 4,500 m (cf. Grytnes and Vetaas 2002). Furthermore, useful plants (e.g., Tibetan medicines, non-timber products, traditional foods, fodder, etc.) are most abundant in alpine meadows. As a result,

climate change that threatens alpine plants also endangers a significant portion of Earth's unique biodiversity and of biodiversity useful to humans.

Climate models and data for the Himalayas present ominous results; for example, nival areas are shown to have decreased rapidly since 1960 and are predicted at present rates to disappear in 159 years (Yue *et al.* 2005). The Intergovernmental Panel on Climate Change (IPCC 2007) released reports including projections for climate change in the Himalayas with high model agreement for temperature increases of 5–6°C and precipitation increases of 20%–30% by 2050. In themselves these changes will be traumatic, but furthermore, the Himalayas and the Tibetan plateau are drivers of monsoon patterns, air circulation, ocean currents, and world climate patterns (Shrestha *et al.* 1999). Thus, the dramatic climate change in the Himalayas will affect over a billion people in Asia who depend on water from monsoons and the rivers with origins in these mountains (Singha and Kumara 1997), as well as the rest of the world affected by ocean currents which are driven by Himalayan orographic lifting of major air masses and currents.

Contemporary photographs, when compared with historic photos taken in the Himalayas up to one hundred years ago (repeat photographs by Baker and Moseley 2007), document extraordinary glacial retreat and treeline and shrub advance, far greater than in other alpine areas of the world. These photographic data substantiate the climate model predictions of exceptional change in the Himalayas.

To monitor the effects of this climate change on Himalayan alpine vegetation, we have joined the Global Observation Research Initiative in Alpine Environments (GLORIA, see www.gloria.ac.at). Responding to the increasingly apparent ecological impact of climate change in alpine environments, GLORIA developed an effective long-term observation strategy for documenting biodiversity and habitat changes, and also for verifying models and assessing risks (Pauli *et al.* 2009). We (Salick *et al.* 2009) find that biogeography (indeed, sky island biogeography), elevation, and precipitation are the major explanatory variables of alpine vegetation in the eastern Himalayas. In response to these results, we are expanding our studies from the eastern Himalayas westward into Bhutan and Nepal. Firm scientific collaboration for this work is provided by the People and Plants initiative of WWF-UNESCO (<http://peopleandplants.org/>) and the Flora of Nepal and Flora of Bhutan Projects of the Royal Botanic Garden Edinburgh (<http://rbg-web2.rbge.org.uk/nepal/floraofnepal/index.html>). These data not only will provide baseline data to monitor climate change in the critical high alpine zones of the central Himalayas but will also provide detailed information on alpine biodiversity, endemism, biogeography, plant responses to precipitation and elevation gradients, and traditional plant use by indigenous populations. In conjunction with our studies in the eastern Himalayas, these data from the central Himalayas will provide a broad biogeographic range of more than 1,500km, over which to analyze these trends.

To GLORIA's ecological mandate, we have added ethnobotany to ask, "What are the human impacts of climate change in the Himalayan alpine?" (Byg and Salick 2009, Salick *et al.* 2009). As noted above, useful plants are most abundant in the alpine (Salick *et al.* 2004). Furthermore, traditional Tibetan medicine includes many alpine plants (Salick *et al.* 2006, Byg *et al.* 2010) and traditional Tibetan land use depends on alpine meadows for grazing (Salick *et al.* 2005). Thus climate change threatens not only alpine plant diversity but also Tibetan peoples and their traditional ways of life. Tibetan people are greatly affected and gravely worried by climate change (Salick and Byg 2007, Byg and Salick 2009). Not only are their sacred snow mountains and glaciers melting, but Tibetan crops are failing, their food is spoiling, and diseases and pests are multiplying. One very knowledgeable Tibetan complains that climate change is making traditional Tibetan culture ill-adapted to our warmer world: traditional Tibetan clothing is too warm and traditional Tibetan food is too fatty and spoils too quickly for the present warmer weather.

Many rare, endemic alpine Tibetan medicinal plants are threatened both by over-harvesting and by climate change (Law and Salick 2005, Salick *et al.* 2007, Byg *et al.* 2010, Law *et al.* 2010). Our results from the eastern Himalayas suggest responses to global warming similar to those documented in the Alps (Pauli *et al.* 2001), so that we may expect the demise of some of the most threatened, slow-growing, endemic plants (e.g., the snow lotus, Law and Salick 2005) and increases of the most common "weedy" species, which would further threaten one of the biodiversity hotspots of the world (MacKinnon *et al.* 1996, Mittermeier *et al.* 1998). Beyond snow lotus, we are expanding our studies of other threatened and endemic species and their responses to climate change, both changes in distributions and phenologies, including endemic *Fritillaria* and *Rhododendron* species. There are similar studies in other mountain regions of the world (e.g., Dunne *et al.* 2003).

Tibetan perspectives on climate change are revealing (Byg and Salick 2009, Salick *et al.* 2009). Almost all Tibetans in our studies recognize climate change, especially glacial retreat, treeline and shrub advance, variable rainfall patterns, and warmer temperatures. However, they have little idea about the cause. They attributed cause to such factors as lack of prayer during the Cultural Revolution, to invasion of non-Tibetans, or to pollution (spiritual and/or ecological pollution). Many Tibetans worry about the implications of climate change and feel powerless. One 85-year-old woman with her great-grandson (Figure 19.6a) fretted, "I am worried that the earth will be destroyed if the snow disappears completely." Offerings and prayers are ceremonially presented to *Klu*, a Tibetan water god (Figure 19.6b), in order to control weather and disease. Tibetan monks struggle to prepare traditional Tibetan calendars that represent the present climatic condition as well as spiritual situation. Nonetheless, Tibetans are adapting to climate change very quickly. They now grow grapes (originally grown by French monks within sheltered churchyards in the eastern Himalayas), produce wine, and even



Figure 19.6. Tibetans recognize and respond to climate change. For example: this 85-year-old woman with her great grandson (left) voices her fears, “I am worried that the earth will be destroyed if the snow disappears completely”; offerings and prayers are ceremonially presented to *Klu*, a Tibetan water god (center), in order to control weather and disease; Tibetans adapt to climate change by growing grapes and producing award-winning ice wine (right).

specialize in ice wine, garnering second prize in an international ice wine contest (Figure 19.6c). Also, Tibetans mitigate climate change through afforestation (see also REDD 2009), yearly incorporation of huge quantities of organic matter into soil (see also Lal 2004), and conservation of biodiversity and carbon sequestration in Tibetan sacred areas (Anderson *et al.* 2005, Salick *et al.* 2007). Indigenous peoples’ perceptions, adaptations, and mitigations of climate change are found throughout the world (Salick and Byg 2007, 2009a).

8 Conclusion

So we see that indigenous and traditional peoples create, manage, and conserve biodiversity and perceive, adapt to, and mitigate climate change. These are invaluable genetic and ecosystem services benefiting the rest of humanity and our planet Earth. These peoples merit a voice in international fora, particularly in the Convention on Biological Diversity (CBD) and the United Nations Framework Convention on Climate Change (UNFCCC), and a substantial role in policy formation. They are the ones who have successfully conserved biodiversity and who feel the brunt of climate change. They have much to teach and to offer the world if we can successfully learn to integrate science and traditional knowledge (Fenstad *et al.* 2002). Unfortunately, in contrast to the CBD, the UNFCCC did not include recommended recognition of indigenous peoples and their plights in the face of climate change (see Tebtebba 2010). Future climate change accords must redress this omission.

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20 Land Architecture in the Maya Lowlands: Implications for Sustainability

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The Anthropocene (Crutzen and Stoermer 2001) signifies the elevation of humankind to a force of environmental change equivalent to nature, capable of affecting ecosystems, including the Earth system (Steffen *et al.* 2003).¹ While overwhelming attention has been given to this role in climate change (IPCC 2007), the human impress on the environment is registered throughout the Earth system, especially in regard to the configuration of the terrestrial surface of the Earth (Turner *et al.* 1990). Humankind matches, and in some instances, exceeds nature in determining the land covers of the Earth, and in this role is a large factor in the structure and function of the environment (Vitousek *et al.* 1997). Indeed, anthropogenic biomes (or coupled human–environment systems) dominate about 75% of the ice-free land surface (Ellis and Ramankutty 2008), appropriating about 25% of terrestrial net primary production (Haberl *et al.* 2007).² They change the capacity of the land system to deliver environmental (ecosystem) services (MEA 2005), often with consequences for human uses and livelihoods.

Such change and consequences have long been mimicked at subglobal scales, with highly differential outcomes for human–environment relationships (Thomas 1956, Turner and McCandless 2004). Some coupled land systems have been operating since antiquity, including certain intensive wet rice systems of cultivation that have been in place 4,500 years (Crawford and Shen 1998). Others have fundamentally altered the delivery of environmental services to which the human subsystem has adapted, such as the Mediterranean rimlands (Butzer 2005, McNeill 1992). Yet other coupled systems have failed, especially those involving intensive resource use on small islands or inappropriate water management in arid lands, with and without climate change (Tainter 1988, Redman 1999, Diamond 2005).

The collapse and depopulation of the lowland Maya about 800–950 CE differs somewhat from other prehistoric collapse cases because of its sheer size (i.e., area and population) and the relative heterogeneity of the landscapes involved (karstic uplands, river valleys, and coastal zones). While the Classic collapse was registered throughout the Maya lowlands, the depopulation was not. The heartlands or

central Maya lowlands, however, incurred both a cultural collapse and major depopulation, on the order of 90% of its zenith population (Culbert and Rice 1990). Whatever the precise linkages of factors leading to the demise of the Classic Maya in the central lowlands (see below), the evidence mounts that land architecture played a role. That architecture developed and sustained the ascendancy of the civilization and its large population for more than a millennium before the collapse and depopulation. The central lowlands reverted to a condition, akin to pre-Maya times, which lasted until the last four decades of the twentieth century.

We explore the role of the changing land architecture for the central Maya lowlands as it relates to the Classic Period collapse. Four dimensions of the environmental subsystem are addressed: biotic diversity, invasive species, precipitation, and phosphorus. Special attention is given to phosphorus because of its critical role as a regulating environmental service. As the land architecture changed, so did the capacity of that subsystem to deliver critical services that had sustained the human subsystem for more than a millennium. This diminished delivery may have helped to place the land system at a tipping point in the face of global climate change and societal conflict.

1 Land architecture and environmental services

Land architecture refers to the kind, magnitude, and pattern of land uses and covers for some unit of the terrestrial surface of the Earth. For anthropogenic biomes, this architecture is the result of the cumulative outcome of various human actions (Turner *et al.* 1990, Ellis and Ramankutty 2008) operating on, initially, ambient environmental conditions. It has profound implications for the functioning of coupled human–environment systems, as noted above. In some cases the very services that are essential for the land uses (e.g., pollination, erosion control, or nutrient cycling) are undermined by those uses or their links to other parts of the human subsystem.³

Several examples illustrate this. (1) It is well known that the maintenance of biotic diversity in a landscape depends, in part, on the configuration of that landscape. Patch size, edge density, and connectivity are only a few attributes of a landscape that may reach thresholds of change (i.e., sufficient habitat) that endanger the presence or abundance of biota, the ability of biota to move across the landscape (Mooney 2003, Lindenmayer and Fischer 2006), and the protection of landscape from invasive species (Mooney and Hobbs 2000). (2) Pervasive land changes can disrupt the capacity of nature to deliver a large range of services. For instance, Chan and colleagues (2006) found minimal land areas along central coastal California that score high in delivering seven ecosystem services, suggesting that a complex architecture is required to deliver those services adequately. Human tendencies to simplify vegetation structure within a cover type while fragmenting land covers, creating new mosaics of land cover promise to stress the deliveries of services from the land. (3) Recent studies from Amazonia strongly

indicate that the size and shape of deforestation affect precipitation owing to impacts on convection and humidity (see below): small and large patches of open land may decrease precipitation, whereas intermediate size patches may increase rainfall (Durieux *et al.* 2003, Li *et al.* 2006, Malhi *et al.* 2007). In short, land changes can have precipitation impacts that supersede those of global climate change (Pielke 2006).

While an increasing number of studies demonstrate that land architecture matters in regard to environmental services, much less is known about the trade-offs in the services for different land architectures (Chan *et al.* 2006, Pejchar *et al.* 2007, Brosi *et al.* 2008). Even less is known about the service consequences as these architectures are aggregated or disaggregated to different scales of analysis. Sustainable land architectures, presumably, are those that, for the most immediate proximate linkages, sustain the delivery of services for the intended land uses, and for the distal linkages, deliver low levels of threats to the functioning of the Earth system.

2 The central Maya lowlands and the collapse of the classic Maya

At the height of the Classic Period civilization (*c.* 450–950 CE), lowland Maya dominion stretched across the entire karstic shelf of the Yucatán Peninsula and beyond, through the watershed of the Río Usumacinta (Mexico) in the west and to the Río Copán (Honduras) in the east and to the Maya highlands (Guatemala) in the south. The central Maya lowlands constitute the Classic Period heartland of the civilization, at least in regard to the sheer mass of monumental architecture, the number and density of major city-states and other settlements, and the size of population (Culbert and Rice 1990). To simplify, the central lowlands stretch from the central Petén lakes of Guatemala to central Campeche and Quintana Roo, Mexico, situated between the coastal plains and the eastern tributaries of the Río Usumacinta (Figure 20.1). At 800 CE, this region may have held more than 3–4 million inhabitants, with densities in excess of 100 people/km² (Turner 1990).

This part of the lowlands represents a distinctive physiognomy and ecology relative to other lowland areas (Turner 1990). Most of the central lowlands correspond to the elevational spine of the peninsula, a rolling upland or *meseta* ranging from 150 to 350 masl, with shallow soils (redzinas) and a deep aquifer. Permanent surface water is limited to a few, short, spring-fed creeks and streams and to scattered sinks (poljes) that form shallow *lagunas*.⁴ The north–south gradient in annual average precipitation creates an ecocline between the more xeric north and humid south, with important implications for the movement of biota. A distinctive winter dry season is sufficiently severe to trigger major leaf loss across the ecocline, its timing and completeness depending on average humidity and annual variability in rainfall characteristics.

The lowland Maya civilization, especially in the central Maya area, collapsed between 850 and 950 CE (with a few locations hanging on to 1,000 CE in some places), an event difficult to explain because of the dramatic loss in population and



Figure 20.1. The central Maya lowlands (circled area) in the Yucatán Peninsula.

the failure of that population to recover – one of few large areas in the world which, over the long run, witnessed one rise and fall of population (Turner 1990, Whitmore *et al.* 1990). Only today has population reached levels (c. 35,000) in the northern part of the central lowlands commensurate with the earliest periods of ancient Maya occupation of the region. Understanding of the complex, interactive causes of the demise of the central lowlands began to take shape in the 1970s (Culbert 1973, Lowe 1985), focused on environmental and social stresses created by land pressures and warfare. Global climate change has been added more recently as the evidence mounts for a major spike in aridity coinciding with the collapse phase (c. 800–1000 CE) (Hodell *et al.* 1995, 2001, Gill 2001, Haug *et al.* 2001).⁵

Climate was not the only environmental change in the Maya lowlands, however. The Maya severely deforested large portions of the lowlands, especially in the central lowlands, evidenced by repeated paleoecological work demonstrating a profound loss in arboreal pollen during the Classic Period. The resulting open, karstic terrain changed habitats for biota, nutrient cycling, and surface hydrology, among other factors. Deforestation led to an initial (Preclassic Period) increase of sediments delivered to water bodies, the evidence for which is especially strong among the rivers of the coastal plains in Belize (Deevey *et al.* 1979, Hansen *et al.* 2002). While this erosion was ultimately brought under control by the Classic

Period (Beach 2002), the dominance of secondary-open vegetation, including ferns, marks the pollen and spore records (Leyden 2002).

The evidence mounts that this deforestation was matched by a land architecture commensurate with the number of city-states and the large size of the population that stretched across the lowlands. By the time of the collapse, the Maya pursued a range of cultivation practices, some intensive on uplands and in seasonal wetlands, others less so, as well as maintaining substantial tracks of exurbia-like orchard-gardens and managed forests (Folan *et al.* 1979, Gómez-Pompa *et al.* 1987, Whitmore and Turner 2001, Turner *et al.* 2003). Access to water was critical, and reservoirs, large and small, were constructed across the landscape, as well as water harvesting systems built into large settlements (Scarborough and Gallopin 1991, Lucero 2006).

This expansive and intensive land-use system developed over centuries, obviously with success, given the sustained growth in population, wealth, and power of Maya city-states. It is evident, however, that the maintenance of the land systems, including reservoirs and managed forests, required substantial labor to maintain and expand. For cultivation this labor was surely linked to the application of night soil, algae, or other potential soil nutrient replacements and to the combating of weeds, especially ferns, pests, and plant diseases (Gómez-Pompa and Kaus 1999).

By the Late Classic Period, the coupled system, especially in the central Maya lowlands, was apparently encountering stress, and this stress was amplified by a major spike in aridity occurring between 800 and 1000 CE. Given that the Maya occupation and cultural ascendancy took place under a prolonged period of climatic desiccation, including mini-spikes in aridity or drought interludes, what would have made this spike special?⁶ One confounding factor was a prolonged conflict between Tikal (north-central Petén) and Calakmul (southeastern Campeche) that lasted over a century and forced all the adjacent city-states to take sides (Martin and Grube 2000).⁷ This conflict likely sapped large amounts of labor and management away from the maintenance of the land system that had heretofore supplied sufficient environmental services. The problem is that this conflict ended by about 680 CE, providing multiple generations to recover before the collapse ensued. Also, as with prolonged drought, the Maya had much experience with warfare (Webster 2002). In this case, however, the recovering generations had to combat the most intensive drought experienced by the Maya within the legacy of the land architecture they devised to support themselves.

3 Limits of the environment subsystem

3.1 Biotic diversity

The central lowlands ecocline is associated with the flow of species between the xeric and humid forest biomes of Yucatán and Central America, respectively. Virtually no work has been undertaken on the role of different magnitudes and patterns of

disturbance on this movement or the implications for specific fauna. Recent work hints that *Manilkara zapota* (zapote) may be a keystone species inasmuch as its fruit serves as a critical dry-season food source for top herbivores in the region (Rivera and Calmé 2006, Reyna 2007). Zapote takes more than 25 years to reach reproductive maturity; thus a landscape replete with open land or young, successional growth significantly reduces the presence and abundance of this vital food source for larger fauna. These fauna were critical protein sources for the Maya. Indeed, if the landscape were as open and as densely occupied as we believe (below), the availability of larger fauna may have been severely depressed, save perhaps for edge grazers, such as deer. It is interesting to note, however, that Maya sites are not abundant in faunal remains (e.g., White 1999, deFrance and Hanson 2008), and that the paleopathology evidence does not necessarily support evidence of major dietary stress building towards the time of the collapse (Wright and White 2005).

3.2 Resistance to invasives

Today, virtually all opened and cultivated land is potentially invaded by bracken fern, which has increased in area fourfold over the past 20 years in southern Quintana Roo and Campeche, Mexico (Schneider 2004, 2006). Repeated burning of the landscape favors its propagation and persistence, and an open fragmented landscape favors fire. Despite the paucity of attention paid to them, fern spores are present in the paleo-record for the Maya lowlands and appear to increase with other disturbance indicators, such as maize and weed pollen, throughout ancient Maya occupation (Rue 1987). If we are correct, bracken fern would have been a labor-intensive problem confronting Maya cultivation. Today, farmers must combat the fern early and often to keep it from taking over cultivated fields (Schneider 2006), and they often abandon plots rather than extend the labor costs to combat the fern.

3.3 Precipitation

The ocean may play a more important role in supplying atmospheric moisture to the Yucatán Peninsula than it does in the interior Amazon (above). Nevertheless, some portion of the rainfall in the central lowlands must be derived from moisture cycled through the vegetation. Thus, we assume that rainfall in the central lowlands may be subject to constraints similar to those observed in the Amazon: that clearings of less than 100 km² and greater than 1,000 km² are likely to result in reduced rainfall, and that clearings between 100 km² and 1,000 km² are likely to result in enhanced rainfall (Durieux *et al.* 2003, Li *et al.* 2006, Malhi *et al.* 2007). The one issue we have not resolved is the degree to which a deforested patch may be sprinkled with forest fragments and still be considered an open patch from the perspective of altered energy and water exchange. We assume that modest forest patches (c. 5 km²) are sufficient to alter the energy balance, thus “breaking up” an otherwise open patch.

3.4 Phosphorus

The loss of phosphorus (P) was proposed 30 years ago by Deevey *et al.* (1979) as having played a role in the collapse, based on the paleo-record of increasingly high levels of P loadings in lakes at the base of the central lowlands (Binford *et al.* 1987). Interest in the role of P has been renewed by recent studies indicating the substantial loss of available soil P in the Maya lowlands, registered by deforestation and slash-and-burn cultivation (Lawrence *et al.* 2007, DeLonge *et al.* 2008), making it a leading candidate to be the limiting nutrient in the biophysical system. Phosphorus is believed to limit productivity in many intact tropical forests (Vitousek 1984) because of the constraints imposed by old, highly weathered soils (Walker and Syers 1976). The current soils of the central lowlands are highly weathered, rich in organic matter, and thin (typically 100 cm or less).

A few assumptions are central to our assessment of the effect of Maya land architecture on P stocks. First, we assume that the P cycle is largely in equilibrium, such that inputs to and outputs from the available pool are equal. Not all P is available to plants. In the crop root zone of Maya soils, about 15% is available on annual to decadal timescales (Diekmann 2004). Another 28% is organically bound, and may exchange with the available pool; over half of the P is more tightly bound to or within soil particles. This large pool includes P that slowly becomes occluded within clays, moving from the available to the unavailable pool. The process of occlusion is a major loss pathway for P over centuries to millennia (Walker and Syers 1976); loss to occlusion may be exacerbated by heavy land use (Garcia-Montiel *et al.* 2000). Phosphorus is not lost through gaseous emissions, although P may be bound in soot and ash that is entrained into the atmosphere during fire and transported elsewhere in the landscape or the region (Kauffman *et al.* 1993). We assume fire has always been used to clear land in the Maya area. Given the dominance of cultivated land and thus the prevalence of fire, we believe P lost from one area would likely be replaced by P deposited from biomass burning upwind. Losses due to leaching through the soil profile are currently quite low (Lawrence *et al.* 2007) and presumably were so in Maya times.

In addition, our assumption is that on Maya arrival in the lowlands, outputs to leaching and occlusion were balanced by inputs of new P in dust. Recent work has shown that intact forest canopies enhance collection of this dust (R. Das, D. Lawrence, P. D'Odorico, and M. DeLonge, unpublished, Lawrence *et al.* 2007). Initial studies suggest that compared to bulk deposition in rainfall, mature forest canopies trap an extra 1 kg P per ha per year. Thus we assume that the 1 kg P added every year was balanced by a 1 kg P loss to occlusion or leaching. This amount represents about 1% of the available pool and about 0.2% of the total pool in the top 30 cm of current forest soils.

On top of this equilibrium P scenario, how P stocks would have changed during cultivation under the Maya must be considered. We focus on the loss of dust-P inputs due to the major reduction in forest canopy and the loss due to export of P in harvest. Both shifting cultivation and intensive agriculture were practiced by

the Maya, but we believe the latter dominated, especially during the late Classic Period. We assume that intensive cultivation was highly efficient, resulting in zero losses to harvest as a result of perfect replacement of harvest losses with night soil, animal manure, or other composted organic material. Because intensive cultivation resulted in a very low plant canopy, however, losses to leaching and occlusion were not matched by dust inputs. Thus, a net loss of 1 kg P per ha per year was registered.

Inputs of dust P were higher under shifting cultivation, depending on the length of the fallow. In the first four years of fallow, dust inputs are assumed to be approximately 0.7 kg less than in mature forest; in years 5 through 11, 0.5 kg less; and in years 12 through 16, not different (see Lawrence *et al.* 2007). We assume that for the early period (1000 to 600 BCE) a 16-year fallow cycle was employed (1–2 years of cultivation followed by 14–15 years of fallow, a conservative estimate given claims that long-fallow is a product of steel cutting tools; Denevan 1992). From then on, we assume what we observe today: a 7-year cycle. Because shifting cultivation is by definition not intensively managed, we assume that harvest losses were not replaced, amounting to a 5 kg P per ha loss per cycle. For the long fallow system, 44 kg P per ha per century was the net loss; for the short fallow system, 66 kg P per ha per century.

For this exercise, our assumption is that the Maya may have allowed one year of fallow (to alleviate pests) for every five years of intensive cultivation. Thus, modeled losses for the intensive system were 99 kg P per ha per century. In neither case do we explicitly consider losses to erosion; we believe the failure to balance dust P inputs covers potential erosion losses. We know that erosion occurred, especially during the first millennium of Maya civilization (Deevey *et al.* 1979).

Finally, our assessment of the effects of Maya land architecture effects on P stocks depends on an assumption about how the landscape grew over time. We use a simple exponential model to predict increases in the amount of land under cultivation. Rates were constrained to yield a pan-Maya world (of which the central lowlands were an exception) that was 70% forested and 30% open in 950 CE and to mirror our understanding of major shifts in population and technology. From 1000 to 600 BCE, shifting cultivation alone was practiced, and it expanded at a relatively slow rate. In 600 BCE, intensive cultivation was introduced. Both it and shifting cultivation continued to grow slowly, at the same rate, until 450 CE. From 450 to 950 CE, growth was more rapid, especially for intensive cultivation. In our model, once under cultivation, land remained under cultivation. We kept track of cumulative P losses (per century) based on when an area came into cultivation and under which system (intensive or shifting cultivation). In this model, however, the spatial pattern of deforestation is not specified. We suggest that once central settlements were established, deforestation probably proceeded as an outward expansion from many independent loci in the landscape, the precise pattern influenced by the presence of upland vis-à-vis wetland and savanna soils. We discuss one scenario below that considers a much more open landscape at a smaller scale, with extensive forest buffers between patches of similar land use density.

4 Changes in land architecture

We illustrate the changing land architecture by way of examining a small portion (c. 1,400 km² or 6%) of the central Maya lowlands situated in southwestern Quintana Roo and southeastern Campeche, Mexico. The area in question is situated in the middle of the north–south ecocline. It supported a large Classic Period population with the large city-states of Becan and Río Bec residing to the west and south, respectively. Today the area constitutes part of the lands surrounding the Calakmul Biosphere Reserve, itself an integral component of the MesoAmerican Biological Corridor.⁸ The area depicted resides fully in the forest type favored by current farmers (medium statured and medium humid) and apparently by the ancient Maya as well as attested by the abundance of former settlements and agricultural features in the area (below).

4.1 Pre-Maya

Figure 20.2 depicts the “natural” land architecture that the Maya encountered in the example area. To simplify, we reduce the land covers of the architecture to four categories – upland forests, seasonal wetland forests, inundated savanna-marshes, and water bodies – that more-or-less prevailed throughout the central lowlands. The upland forests were supported by organically rich redzina soils.

At the time of Maya entry, hurricanes were the major disturbance to the forest (Boose *et al.* 2003); significant hurricane blowdowns have been documented during the past century for the area illustrated. Assuming only minor areas of blowdowns, the Maya encountered an intact ecocline with large corridors for the movement of biota. Projected keystone linkages, such as that between the zapote and tapir (plant dispersed by the animal) were intact. Under this scenario, bracken fern was likely to have been restricted to open areas from forest blowdowns. Invasion was suppressed by shading from secondary growth, because fires were less prevalent in a mostly intact forest. In addition, the intact mature forest would have maintained high rates of evapotranspiration relative to any other land covers, suggesting positive feedbacks on local atmospheric moisture.

P inputs from atmospheric dust – blown from Africa – likely waxed and waned with large-scale climatic changes in the extent of the Sahara and small-scale variation in atmospheric circulation patterns (Swap *et al.* 1992, Okin *et al.* 2004). Under our equilibrium scenario, P inputs matched losses to leaching and occlusion, except following hurricanes and small-scale disturbance (e.g., tree death).

4.2 Classic Maya

Figure 20.3 illustrates the land changes in place at the height of the Classic Period occupation, in which local to regional population densities ranged as high as 150 people/km² for the mapped area (Turner 1990). By this time, the region was

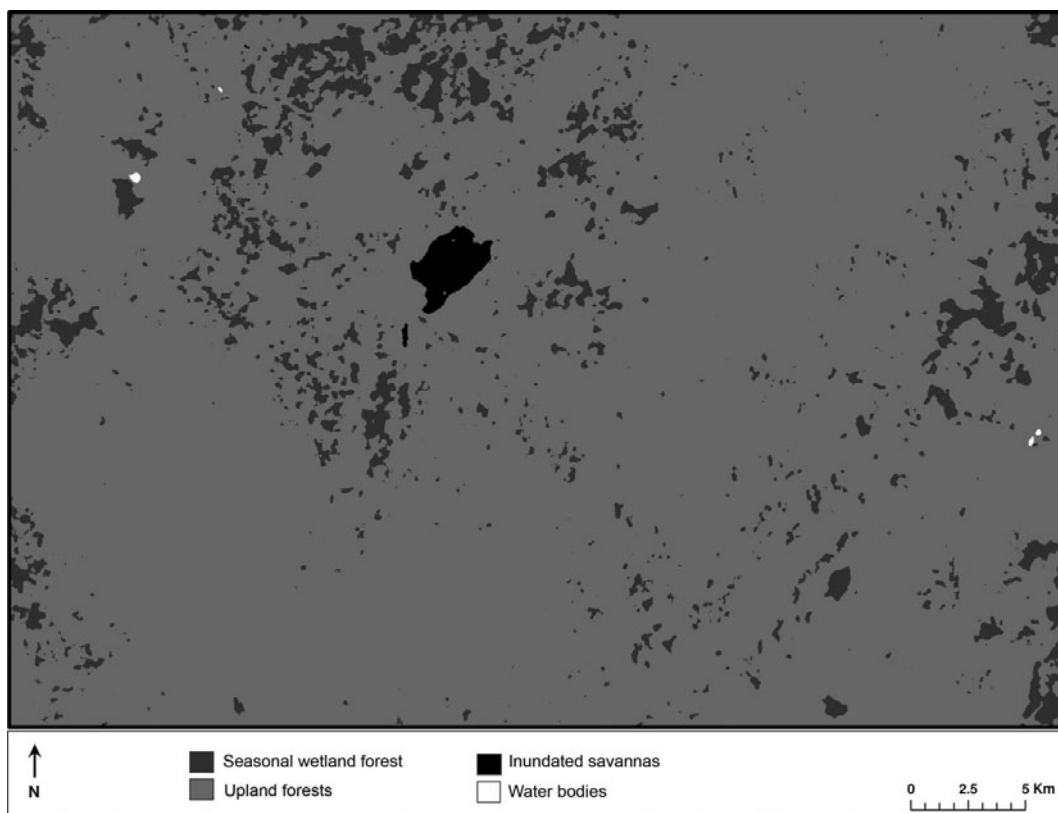


Figure 20.2. Simplified Pre-Maya Land Architecture: example from a part of the Central Maya Lowlands.

replete with large to small settlements, as well as rural areas scattered with hamlets and farmsteads, typically on hill crests. Large portions of the former upland forests were opened for cultivation, 80% of which was likely some form of permanent or near-permanent (intensive) cultivation given the nearly ubiquitous relicts of farmsteads with lands covered by stone walls and terraces.⁹ The settlements and farmsteads were undoubtedly planted with the orchard-gardens reported by the Spaniards with first contact (early 1500s) of the Postclassic northern Maya (Whitmore and Turner 2001).

Unfortunately, we do not know the locations or total area of managed forests (ad hoc distribution in Figure 20.3), although there is strong reason to believe they were present. This belief comes from the extremely high fuel demands of the Maya, not only for cooking but for the massive amounts of mortar used in construction. Part of this demand was likely met by use of wood taken from seasonal wetlands (*bajo* forests in Figures 20.2 and 20.3), but not all. Mahogany and Spanish cedar, used as lintels in the construction of large architectural features, do not grow in the wetlands.¹⁰ The pollen record confirms that managed or unmanaged forests were not dominant on this landscape (above). Our land

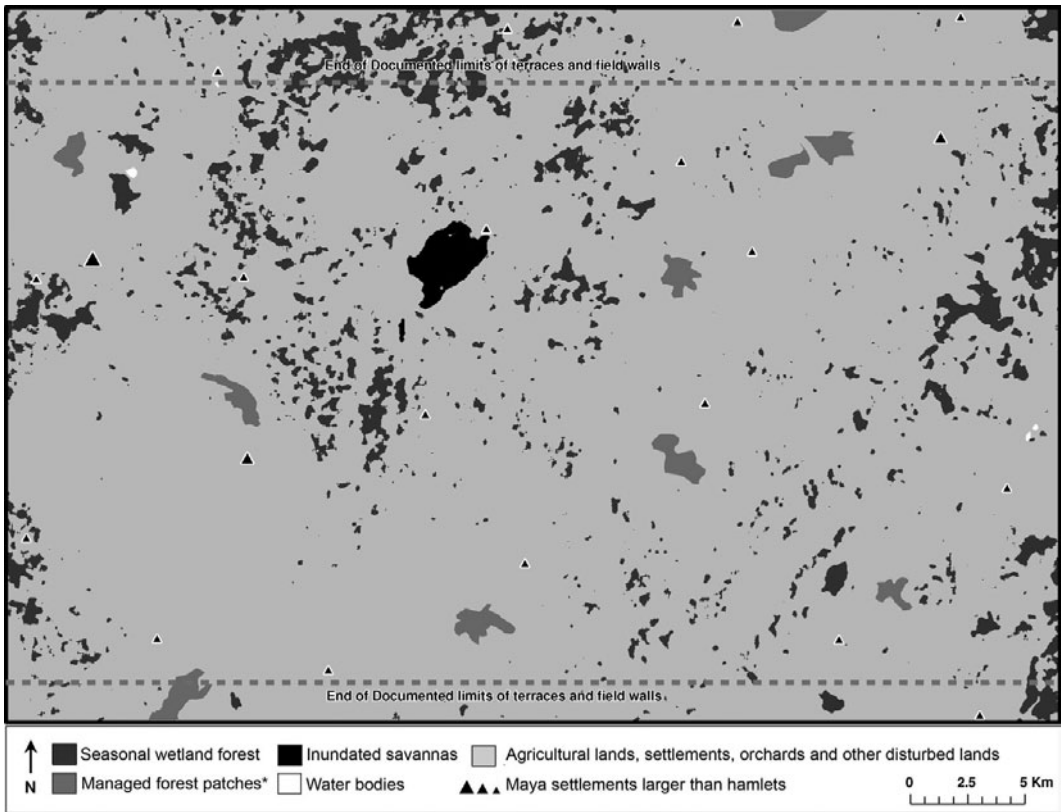


Figure 20.3. Simplified Classic Period land architecture: example from a part of the Central Maya Lowlands.

architecture reflects approximately 80% open lands, with about 15% in unmanaged *bajo* forests and 5% in managed forests or orchards. At the scale of the central Maya lowlands, however, buffers of unmanaged forest between areas of dense occupation, such as our 1,400 km² sample area (Figures 20.2 and 20.3), would result in about 60% of the area being forested and 40% under cultivation. At a larger scale still, that of the entire Maya world, including far less populous areas, we imagine the forested area might have reached 70%.

What were the impacts of this land architecture? Unless the Maya were astute about linking *bajo* forests with managed forests and orchards, the upland forest corridors were lost, raising questions about movement of biota across the north–south precipitation gradient. The wetland forests perhaps served as refugia for some upland forest tree species, but not zapote (above) and ramón (*Brosimum alicastrum*), another fauna-important fruit-bearing species (Pérez-Salicrup 2003). Indeed, save for managed forests, the keystone species zapote and ramón were reduced significantly in extent and abundance as their favored habitat was taken by farmers. The presumed reduction of these dry season food sources would have affected fauna, but given the projected landscape, just how much fauna would

have been present given the land changes and stress from hunting is an open question. As noted above, however, site-linked fauna remains in the central lowlands are sufficiently sparse to render chronological assessments of this food source difficult. As well, the few osteological studies of the ancient Maya, also reflecting the paucity of remains found to date, have not yielded evidence that the Classic Period Maya suffered from extreme nutritional or protein stresses (White 1999).

Regardless, bracken fern surely plagued Maya farmers, consuming considerable management attention and labor. The impact of bracken on the local soils is understudied, but the species tends to be associated with low P soils. Whether it is more successful on low P soils, or whether it somehow induces a loss of P has not yet been determined.

As depicted in our sample area, the land architecture in the northern part of the central lowlands (Figure 20.3) most likely had a negative effect on rainfall. About 80% of this area was open, yielding a total open area of about 1,100 km². Were this area in one large block, it would be about the maximum size that actually enhances rainfall (1,000 km²). Because of the existence of *bajo* forests, however, the open area is not one continuous block. In fact, most of the open patches are substantially smaller than 100 km², the lower limit on the size of openings that enhance rainfall. Although the largest open area is perhaps 350 km² (see lower left of Figure 20.3), most of the open area is broken up by small patches of *bajo* forest. In our rendering of the land architecture, managed forests similarly break up larger open areas, especially in areas with less *bajo* forests. Nevertheless, we note that the fragmentation of otherwise large open patches does not depend entirely on our placement of managed forests. The natural contours of the landscape (with depressions supporting *bajo* forests) and the preference for cultivating uplands limit the size of deforested patches to a size that reduces rainfall. Across the landscape, rainfall may have been enhanced in some areas while diminished in others. We believe the net effect for the area in Figure 20.3 would have been negative. This claim would hold for most of the central Maya lowlands at higher elevation where the area of *bajos* decreases and in which there is little evidence that the wetland forests in them were denuded.

According to our model, P would certainly have been deficient on much of the landscape. Half the area under cultivation would have lost more than 100 kg P per hectare. The rest would have lost at least half that much. One fourth of the area would have lost more than 200 kg P per ha (5%–6% each would have lost > 300 or > 400 kg P per ha). These losses are substantial. We have added the lost P to stocks observed in current unmanaged forests to characterize the pre-Maya soils (making the assumption that these soils have not “recovered” despite a millennium of dust P inputs). For the range of the best to the worst soils across the central Maya lowlands, 100 kg of P represents 73%–100% of the pool of available phosphorus in the crop zone of plants (top 15 cm). Because it is the most labile, we assume this pool is not only most readily available to plants, but also most easily lost to leaching and occlusion.

On more marginal lands, the only way to sustain yields under intensive cultivation would have been to manage carefully the annual inputs of recycled P (from night soil, animal manure, or compost). It is not clear that yields could have been maintained under shifting cultivation, as farmers would have depended on P supply from slower pools. A loss of 200 kg or more of P represents, at a minimum, 17%–100% of the organic P pool in the surface soil. Thus, in a quarter of the landscape, not only had the entire pool of available P been lost, but so had a substantial portion of the pool that might have replenished it. At the time of the collapse, the capacity of the soils to supply P to crops was certainly precarious over much, if not all, of the cultivated landscape.

It seems highly likely that the land architecture affected the P supply capacity, especially in the central lowlands at large. For example, assume that permanent (intensive) cultivation originated and continued to dominate land use near the population centers (e.g., triangles in [Figure 20.3](#)). More distant lands were taken to more intensive practices later, and would have suffered fewer P losses. By the time of the collapse near-settlement lands may have lost up to 200 kg P, even with management practices to offset losses. Such losses would have increased the value of more distant land, setting up potential conflicts among settlements for the areas in question. Within any polity, institutions to adjudicate the competition for this land surely prevailed to avoid conflict. The central Maya lowlands at large, however, were composed of major city-states and their hinterlands, with no apparent pan-Maya governance structure. Conflict over the lands between major city-states, presumably those with less losses of P, may have contributed to Maya warfare.

On reflection, the coupled human–environment system may have been reaching a tipping point that would have been crossed with any major disruption in the management system, such as might be expected to follow from prolonged societal conflict, as registered in the Tikal–Calakmul war. Subsequent attempts to recover the cultivation and water systems were confronted by the labor and management costs of bracken, severe loss of soil P, and intensive desiccation of the landscape.

5 Summary and conclusions

Land architecture – kind, magnitude, and spatial pattern – affects the capacity of landscapes to provide the environmental services expected by the land manager. The ancient Maya entered a lowland environment abundant with fauna, and supplied with sufficient nutrients, especially P, and water to support an increasing population and standard of living, registered by the scale and quality of monumental architecture present there. Adjusting to various mistakes, such as upland erosion, Maya adaptations in cultivation, water storage, and land management in general sustained overall population and economic growth in the central lowlands, leading to highly managed land architectures by at least the latter stages of the Classic Period, if not before. Once established, alternative architectures were

rendered difficult, without major implications for the size and well-being of the population and city states. The human–environment path taken simply reduced the options available to the Maya as higher levels of stress were encountered from climatic drought and, probably, reductions in labor and management given to food and water procurement systems.

This interpretation points to the path-dependent characteristics of the coupled human–environment system in the central Maya lowlands. In addition, we suggest that stresses placed on that coupled system were partly derived from the synergy of its subsystems which reduced the capacity of the environmental subsystem to maintain regulating and supporting environmental services (e.g., nutrient cycling), and ultimately, provisioning ones. The collapse apparently involved both exogenous (global climate change) and endogenous (land architecture consequences) factors. Fundamentally, the impacts of climate change registered a cultural collapse largely because of the legacies of the coupled system registered in the landscape architecture.

Finally, it is noteworthy that this explanation of the Classic Maya collapse does not explain the long-term impacts on occupation in the region. The forest (environment subsystem) recovered, if altered in species abundance (e.g., Lambert and Arnason 1982). The human subsystem did not, as the region has remained ephemerally populated to this day.

6 Acknowledgments

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Notes

- 1 The human role in the Late Pleistocene megafauna extinctions (Martin 2005) was global in scope. In addition, Ruddiman (2005) argues that human-induced deforestation and agriculture was of sufficient magnitude to affect atmospheric CO₂ and CH₄ by about 8000 BP and 5000 BP, respectively. Much of the expert community is skeptical of this claim, however (e.g., Broecker and Stocker 2006).
- 2 Coupled human–environment systems have also been labeled social–ecological systems and coupled human–natural systems (Liu *et al.* 2007).
- 3 Ecosystems at various scales provide provisioning (e.g., food stocks), regulating (e.g. climate stability), supporting (e.g., nutrient cycling), and cultural (e.g., preferred

- landscapes) services to society (MEA 2005). While first labeled ecosystem services, large parts of these services are affected by or emanating from parts of nature that are not technically ecosystems. Thus our use of the term environmental services.
- 4 Rivers exist to east–southeast and west–southwest of the central lowlands, especially at lower elevation, off the *meseta*. A few, fault-derived, deep-water lakes also exist, especially on the southern edge of the central lowlands.
 - 5 It is noteworthy that proponents of the geographic factor (i.e., environmental determinism) invoked climate change as the cause of the Maya collapse as early as the first part of the twentieth century (Huntington 1915). In this case, however, the cause was interpreted as increased humidity, which would have amplified problems with malaria and other vector-based diseases.
 - 6 Also, the northern lowland Maya occupied a more xeric environment than that in the central lowlands. While they too experienced the pan-Maya cultural collapse, they did not depopulate but continued to thrive (Chase and Rice 1985, Culbert and Rice 1990).
 - 7 A nontechnical account of this conflict can be found in Mann (2005).
 - 8 The area depicted here is meant to be illustrative only. We selected it because one of us (Turner) exhaustively surveyed the area in the 1970s for relics of ancient Maya land uses, and both of us are part of the long-standing Southern Yucatán Peninsular Region project that examines contemporary land change dynamics in the area (<http://earth.clarku.edu/lcluc/>).
 - 9 The dashed lines in Figure 20.3 represent the range of observed stone walls and terraces established in the past work in the area (Turner *et al.* 2003). Systematic sampling reveals that features exist to the north and south of the limits noted.
 - 10 Below 150 m elevation some wetlands, especially along coastal rivers, were used for cultivation (Turner *et al.* 2003). No features indicating the use of wetlands have been found in the area depicted here.

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21 Agrobiodiversity and Water Resources in Agricultural Landscape Evolution (Andean Valley Irrigation, Bolivia, 1986 to 2008)

Karl S. Zimmerer

This chapter examines the evolution of agricultural landscapes that involve the interactions of agrobiodiversity and water resources. My goal is to identify and evaluate the environmental flows and human–environment management connections, referred to here as “linkages”, between these two types of resource use within dynamically evolving agricultural landscapes that incorporate crop irrigation. My analysis is focused on key processes and spatial patterns of landscape connections (involving human activities as well as crop, water, soil, and vegetation components) and, also, on determination of the limitations that constrain each of the primary links. This topic holds increased importance due to the landscape transformations that increasingly determine the viability of agrobiodiversity (Wood and Lenné 1999, Brush 2004). One prime example, and the focus of this presentation, is landscape evolution consisting of agrobiodiversity in contexts of irrigated agriculture (Zimmerer 2010a,b). Many such changes are propelled through major shifts in policies of water resource management (e.g., the partial end of the “big dam” era described below), as well as the expanding impacts on water resources resulting from climate change and energy resource development (WCD 2002).

The chapter begins by introducing the three elements of a proposed framework for evaluation of the ongoing evolution of agrobiodiversity dynamics within irrigated landscapes. These elements are (i) agrobiodiversity and irrigated landscapes; (ii) water resource management and current irrigation development policy; and (iii) landscape-based analysis of spatial parameters.

Analyses are then presented of four linkages that are identified as functioning as strong shapers of these elements in tropical mountain environments (using the case of the Calicanto irrigated landscape in Cochabamba, Bolivia): (i) management of water-related risk in the location and strategies of agrobiodiversity cultivation; (ii) fertility management of irrigated soils involving nutrient transfers within the landscape; (iii) livelihood diversification involving non- and off-farm work activities that are recognized as having a conditional relation to

agrobiodiversity viability (neither a priori opposed to continued agrobiodiversity production, nor a priori in support of this type of outcome) and (iv) the landscape role of irrigation-related woodland matrices that interact with agrobiodiversity production through water, nutrient, and gene flow interactions. Next I discuss the changes of agrobiodiversity–water interactions in dynamic agricultural landscapes. Specific conclusions focus on identification of the level of resilience (with limits) of the above components of dynamic landscape evolution involving Andean irrigation development and high-agrobiodiversity crop complexes. General conclusions extend beyond resource and landscape resilience per se to overarching connections of agrobiodiversity and water resource development.

1 Framework for understanding agrobiodiversity–irrigation landscape dynamics

The Central Andes (Peru, Bolivia, Ecuador) are widely recognized as a global center (or “megacenter”) of agricultural biodiversity that extends also to the landscapes of “noncenter” areas stretching from Venezuela to central Chile and northwestern Argentina. Farmers in these countries – many of them peasant and indigenous people – create and maintain agricultural landscapes that contain unique geographic concentrations of various crop complexes. Most well known and studied are the high-agrobiodiversity upland cultivation systems of Andean tuber crops and grains (e.g., Andean potatoes, ulluco, oca, quinoa). Less attention has been paid to the intermediate-elevation agricultural landscapes (1,000–3,000 m above sea level). Farmers in these locales create and maintain lower-slope and valley landscapes where high-agrobiodiversity agriculture is present and viable, yet less extensive and less studied than in upper areas. Lower-slope and valley landscapes in the Central Andes provide growing habitats for a large number of biologically unique assemblages of cultivated and uncultivated taxa ranging from Andean maize and Andean common beans (as well as Andean Lima beans and other legume crops) to certain types of squash, chile peppers, and a subset of the Andean potato complex. This study is focused on agrobiodiversity of Andean maize types (taxonomically and genetically distinct) and, to a lesser extent, Andean common beans and Andean potatoes.

Irrigation is typical of many high-agrobiodiversity landscapes in valley farmlands and other intermediate-elevation growing habitats of the semi-arid and sub-humid valleys of the tropics and sub-tropics between Venezuela and central Chile/northwestern Argentina. Widespread use of irrigation in these Andean locales creates a multitude of interactions of water resources with agrobiodiversity. These interactions are both direct and indirect. Direct interactions primarily involve the use of irrigation for crop production. Indirect interactions include the ecological function of irrigation in creating and maintaining nonagricultural habitats, such as canal-side areas, that serve as important habitat for uncultivated agrobiodiversity (so-called “wild relatives” of such crops as Andean common beans and

Andean potatoes). My analysis – presented in the next section – is based on a case study of the Cochabamba region of central Bolivia.

The Cochabamba region provides the most extensive area of high-agrobiodiversity landscapes, much of which is grown under irrigated conditions, and significant opportunities for sustainability policies. (My research includes examination of the development and impact of food-security, agrobiodiversity-promoting, and other agrarian policies of the Morales government in Bolivia, although this topic is not included, aside from general mention, in this chapter.) The case is focused on the Calicanto irrigated landscape and surrounding “High Valley” (Valle Alto) of Cochabamba where I have conducted field studies since 1986. Andean maize, with the occurrence of at least six major types representative of “core Andean” genetic groupings (Sánchez *et al.* 2000, 2006), is the major high-agrobiodiversity crop of the Calicanto irrigation landscape. Other high-agrobiodiversity crop types are Andean potatoes and Andean common beans, although the latter are planted to only a small extent.

Current trends in water resource management and irrigation development policy are generally well represented in the Cochabamba region, including the Calicanto irrigated landscape. These trends are typical of many irrigated Andean landscapes, as well as global trajectories. A pair of characteristic trends is highlighted for the purpose of drawing connections to agrobiodiversity in this presentation. First is the trend toward small- and medium-scale irrigation projects, many designed as either community-based resource management or through establishment of special-purpose irrigators’ associations. Combined environmental, economic, and social rationales have caused this shift away from the “big dam” projects that characterized a majority of irrigation development until the past decade or so. (“Big dam” projects have not disappeared completely, notwithstanding the shift to increasing number of small- and medium-scale projects.)

This trend away from the irrigated landscapes of “big dam” projects, at least in part, is typical of global irrigation development, in which western South America and the Andes are a vitally important area – and Cochabamba and the Calicanto landscape offer a typical local example. Second is continued expansion and intensification of irrigation, and other water resource use, through investments, planning, and implementation of small- and medium-scale projects. In other words, water resource management is increasingly prevalent and powerful in providing one of the primary avenues of landscape change (organizational, technological, and planning-participation) involving agrobiodiversity. The Calicanto landscape, which serves as the foundation of my case study, has been subject to the expansion and intensification of medium-scale irrigation development during the past 20 years (as described below).

The third element in my study is landscape-based analysis using the tools and techniques of Geographic Information Science (GIS) combined with field methods that include crop and plant collecting, sampling, and taxonomic identification, sampling of soil for physical and chemical analysis, and field-level crop mapping. The agro-environmental-gearred field methods were designed and coordinated with

farm interviews and surveys in the Calicanto irrigated landscape. A GIS database has been compiled of the Calicanto irrigated landscape based on the availability of a fine-grain topographic map (2.5 m contour interval) and aerial photographs (1:8,000 scale) that were completed in the period 1989–1993. Data layers of the GIS include topography, agricultural fields, irrigation canals, woody vegetation, river channels, and settlements. (The town of Tarata is located at the upper-end of the Calicanto irrigated landscape. Several smaller villages, such as Arbieta, Villa La Loma, Villa Mercedes, and Mamanaca surround the perimeter of the irrigated landscape.)

GIS analysis of basic spatial parameters includes: (i) the irrigated landscape in the GIS measures approximately 12 km²; (ii) the overall irrigated landscape is estimated to cover approximately 15 km² since topographic map and aerial photograph coverage is not comprehensive; (iii) approximately 3,600 fields occur in the 12 km² section of the irrigation landscape; (iv) approximately 80% of the area consists of agriculture fields; and (v) more than 65 km of canal occur in this section. GIS-based analysis of these parameters of the Calicanto irrigated landscape represents an important advance in studies of high-agrobiodiversity landscapes. These estimates, and other features of the GIS database, are being updated and combined with the analysis of remotely sensed images taken of the irrigated landscape in 2006 and 2008 (detailed below). Preliminary analysis suggests the maintenance of several basic spatial parameters of the irrigated landscape such as field number and canal extent, through to the present. Other spatial parameters are described in the analyses below.

2 Analysis of agrobiodiversity–water interactions in landscape evolution

Risk is common in irrigated agricultural landscapes. Various types of risk are characteristic of small- and medium-scale irrigation. The Calicanto irrigation landscape functioned for hundreds of years – until the mid-1990s – as a system of spate irrigation or so-called hybrid floodwater–canal irrigation. Ephemeral flows of the Rio Calicanto have been channeled, via diversion weirs, in the network of canals consisting of 4–5 primary canals that fed larger numbers of secondary and tertiary canals. A dam and concrete-lined canals were completed in the mid-1990s as part of the “Multi-Purpose Laka Laka Project.” Problems of substantial sedimentation and social conflicts have plagued the Laka Laka Project and led to only partial replacement of hybrid floodwater–canal irrigation. As a result, irrigation risks have continued to play an important role throughout the study period. The primary risks can be synopsized as water surplus/avulsion flooding and water shortages/drought. (The mean value of annual rainfall is approximately 500 mm, which provides inadequate soil moisture for rainfed cropping, so the extent and timing of irrigation are crucial for high-agrobiodiversity crops as the commercial ones that have expanded in the Calicanto irrigated landscape – which consist principally of peaches and alfalfa.) Farmer surveys, interviews, and GIS

analysis are being used to estimate the occurrence of irrigation risk within the Calicanto landscape.

Analysis of irrigation risk dynamics indicate that water surplus/avulsion flooding is most common in the up-canal areas where high flows have sporadically broken through earth-lined canals. By contrast, water shortages/drought occurrences are characteristic of the down-canal areas, where irrigation flows become inadequate or lacking entirely in certain years (and, also, at times within the extended growing season when irrigation is required). Farmers' management of agrobiodiversity has been a crucial source of their capacity to respond to these irrigation risks. My field study results show that water-stress-tolerant maize types have been grown in the down-canal areas (subject to water shortages and drought). Alfalfa and long-maturation maize types are produced in the up-canal areas, which provide a greater supply of water, albeit under conditions of higher risk of excess water. Andean potatoes (the *mishka* or "early crop") have customarily been grown in the mid-canal areas of the Calicanto irrigation landscape, since farmers perceive this "early crop" as vulnerable to conditions of both water surplus and water deficit. In summary, a variety of high-agrobiodiversity crop complexes have helped provide farmers with the capacity to respond to irrigation risk; both these high-agrobiodiversity crops, and irrigation risk, are spatially differentiated, as indicated above, within the Calicanto landscape.

The second area of analysis is the fertility management of irrigated soils that involves nutrient transfers within the Calicanto landscape. Focus here, similar to the one on risk, is on the combined human–environmental and spatial dynamics. Identification of the importance of soil fertility management is an addition to customary and more one-dimensional treatments of irrigated landscapes (with exclusive emphasis on processes of the water resource). Amelioration of soil fertility is crucial to high-agrobiodiversity cultivation in the Calicanto irrigated landscape, reflecting the general importance of soil fertility management in the evolution of tropical agricultural landscapes (Denevan 2001). It is suggested that soil management is a concomitant yet often overlooked component of irrigation involving high-agrobiodiversity crop complexes. In the case of the Calicanto landscape, water flows are sediment-rich as a result of widespread erosion in the watershed that drains into the irrigation area. These irrigation-derived sediments are relatively nutrient poor, although they often are depicted as fertile in general descriptions of irrigated agriculture in Cochabamba. Indeed, the freshly deposited irrigation sediments are unconsolidated and fine grain – a person walking in these fields can easily sink to ankle height.

Farm interviews and soil samples in the Calicanto irrigated landscape indicate the significant build-up of organic matter and nutrient availability (including the modification of soil texture) through the additions of livestock manure. Relatively abundant manure, especially from local dairy cows, has served as a crucial soil amendment providing the fertility required by the high-agrobiodiversity crops, which typically are more dependent on organic-matter-based availability of soil nutrients. This soil nutrient transfer is characterized by an important spatial

dimension within the Calicanto landscape. Farmers with field sites in the up-canal areas have mainly tended to keep dairy cows, which are common in conjunction with the sites of alfalfa cultivation. These farmers benefit economically from payments to secure the sought-after manure, either outright or through arrangements whereby manure is added directly to a field while the livestock graze on crop stubble and weed growth at the end of the growing season. Mobility of livestock reflects the basic spatial axis and direction – from up- to down-canal – of this nutrient transfer. (Maize stubble has long been an important source of fodder for livestock in the irrigated area, although this resource is lessening as a result of expanded peach cultivation.)

Livelihood activities (focused in my study on economic, land tenure, and cultural factors) are central to the evolution of agricultural landscapes. Livelihood processes are often equally or more complex – being multiple, socially varied (including household- and community-level organization) and spatially intricate (e.g., contiguous, gradient-type, and noncontiguous patterns) – than other agrobiodiversity-related functions that are biogeophysical, at least partly, such as water risk and nutrient flow. As a result, analysis of the relations of livelihood activities contributes an important, multi-faceted dimension to understanding agrobiodiversity–water interactions as complex human–environment systems. My study is focused on the linkages of livelihood activities to agrobiodiversity in the context of irrigated farming. In many Andean valleys, including the Calicanto irrigated landscape, livelihood activities are highly diversified and dynamic. Diversification and dynamic change stem from the high level of integration of local farming into product and labor markets that also involve significant non- and off-farm components.

To date analysis is focused on four sorts of livelihood activities that are identified as central to agricultural landscape evolution involving agrobiodiversity–water interactions. The analysis begins with agricultural diversification. The majority of farm households in the Calicanto area hold access – through ownership, rental, and sharecropping – to a total of 3–5 fields, including 1–3 irrigated parcels, which enables them to combine high-agrobiodiversity production (e.g., Andean maize and Andean potatoes) in certain fields with the cropping of peaches, alfalfa, and wheat (in unirrigated parcels) in their other cropping sites (KS Zimmerer and ED Carter, unpublished). Second is the role of field size. GIS analysis indicates that the majority of Calicanto irrigated fields are smaller than 2,000 m² – this small field size is incorporated into agricultural diversification strategies – and that field size tends to decrease in the down-canal direction (contributing to the large numbers of small fields, many with high-agrobiodiversity production, in the distal areas of the irrigated landscape). Third are migration activities, which figure importantly to a majority of Calicanto irrigators. The earning or remittances of labor migration (which is local, national, and international) have continued to be invested, at least in part, in irrigation works, thus enabling a positive impact on high-agrobiodiversity production (such as Andean maize). Fourth is extra-household organization of

irrigation. Canal-based units (known as *suyus* and sub-*suyus*) involve community groups, whose organization and labor inputs have been vital to irrigation (e.g., investment in irrigation works) and, by extension, to high-agrobiodiversity production within the complex landscape and diversified livelihood activities.

The fourth area of analysis is the landscape matrix of canal woodlands and channels that form significant extensions of interlaced uncultivated areas, including suitable habitat for uncultivated crop types (e.g., uncultivated Andean potatoes, uncultivated Andean beans). These woodlands are anthropogenic (heavily dependent on human activities) (Zimmerer 2010a). Numerous tree, shrub, herb, and grass types, along with animals, occur in these canal woodland habitats, which, to a large extent, occur along field boundaries (see also Le Coeur *et al.* 2002). These spatial ecological characteristics, including the influence of anthropogenic effects, and their role in agrobiodiversity–water interactions, have been overlooked until recently. GIS analysis estimates that the woodland landscape matrix makes up approximately 10% of the overall area of the Calicanto irrigated landscape (Zimmerer 2010a).

Water, nutrient, seed, and pollen flows occur between the woodland matrix and the dense patchwork of agricultural fields. Matrix-patchwork transfers of seed and pollen include the uncultivated crop species, which are landscape elements that are widely known about among local farmers. Indeed local farmers possess well-developed knowledge about the ecology, distribution, and properties of the uncultivated taxa (for example the types known locally as *k'ita papa* and *aparuma*, which are the uncultivated Andean potatoes, and *k'ita purutu*, the uncultivated Andean common bean, respectively). Extensive habitat suited for these uncultivated crop taxa occurs along all three primary ranks of irrigation canals – primary, secondary, and tertiary (KS Zimmerer, unpublished). GIS analysis demonstrates a strong elongate tendency of the shape of irrigated fields, which significantly increases likelihood of interactions (including introgression) between the uncultivated areas, including the wild crop taxa, and the patchwork that contains high-agrobiodiversity field production.

3 Discussion: landscape evolution dynamics and agrobiodiversity

Various development trends contribute to the change dynamics of agrobiodiversity–water interactions in the agricultural landscapes of Andean valleys. Water development projects are one of the most powerful drivers of agricultural landscape evolution in these locales (and in arid, semi-arid, and sub-humid environments globally), both during the past few decades and into the foreseeable future. Irrigation initiatives, involving the combination of organizational, technological, and socio-economic change, have become an increasingly major force impinging on agrobiodiversity in the context of landscape evolution. Farmers, landscapes, and agrobiodiversity of the Calicanto area have been affected through the changes of a combined dam and concrete-lined canal

project undertaken in various phases between 1990 and 2002. My study evaluates three dimensions of landscape change dynamics: (i) agrobiodiversity and crop landscape related to irrigation change; (ii) water–land interactions; (iii) agrobiodiversity mosaic of woodland matrix and cropland patchwork. Analysis of the preceding section is being combined with classification and change detection of additional satellite imagery (2006 and 2009 QuickBird images of the study), combined with oral histories, interviews, and crop and vegetation sampling that are focused on landscape-, irrigation-, and agrobiodiversity-change.

Initial findings in each of the above areas are as follows. (i) New irrigation and continued investment of migration earnings is leading to expanded cultivation of peach trees while, at the same time, high-agrobiodiversity Andean maize has continued in local production. Irrigation-related risk rationales are lesser in degree, though still influential, and similar in nature, in leading farmers to rely on high-agrobiodiversity production. (ii) Water–land interactions, which have been modified significantly as a result of irrigation development, are combining with the changes noted in (i) above, in order to lessen the soil fertility mechanisms that are provided through integration of livestock-manuring and high-agrobiodiversity cropping. (iii) Woodland canal matrix, including habitat suitable for uncultivated crop taxa, has remained largely intact (though it is altered in places) and is noticeably persistent in the wake of substantial irrigation development.

4 Conclusions: resilience-with-limits and linkages of agrobiodiversity–water interactions in agricultural landscape evolution

The specific conclusions of my study are focused on estimates of the social–ecological resilience of landscape- and agrobiodiversity-related resource issues examined above (irrigation risk, soil fertility management, livelihood activities, woodland/habitat matrix). The level of social–ecological resilience refers to the capacity to respond to change (Walker *et al.* 2004, Folke 2006). This characterization is based on evaluation of flexibility of the formative processes, especially ones that are mutually reinforcing processes (“positive feedback”), and also initial analysis of diachronic landscape change (1985–2008).

Estimation of the social–ecological resilience of each component entails identification of both adaptive capacity and limits in agricultural landscape evolution. These combined characterizations are: (i) medium–high resilience is characteristic of irrigation risks, to date, due to continued processes and distributions of principal risks (avulsion flooding and water shortages) and demonstrated flexible capacity for agrobiodiversity-based responses (especially the processes that underpin availability of water-stress-tolerant Andean maize); (ii) medium–low resilience is characteristic of soil fertility management based on livestock manuring, since integration of dairy cows (or other manure source) into irrigated agriculture requires large areas of alfalfa and maize production, or some alternative fodder source or fertility-enhancing techniques (e.g., crop rotation), which have limited

flexibility; (iii) medium-level resilience is characteristic of livelihood activities related to agrobiodiversity, since diversification, as a process, offers potential for the flexible support of agrobiodiversity (e.g., investment of migration remittances into agrobiodiversity-supporting irrigation) while, at the same time, these livelihood choices may be shifted to other activities that are currently complementary (e.g., other nonagrobiodiversity-based cropping systems); and (iv) medium–high resilience of canal woodland habitats, including uncultivated agrobiodiversity, that comprise a landscape matrix whose formative processes show significant flexibility in terms of both human management and nonhuman regeneration.

My general conclusion is focused on highlighting the complex relation of agrobiodiversity to irrigation. Using the example of the Calicanto landscape, my findings offer a detailed examination of the ways in which the cultivation of agrobiodiversity is maintained under irrigation. My approach reflects a focus on the interaction of factors associated with both agrobiodiversity and “agrodiversity” (on the latter see Brookfield 2001 and Brookfield and Padoch 1994). Production of agrobiodiversity (principally Andean maize and, to lesser extents, Andean potatoes and Andean common beans) has persisted notwithstanding irrigated-related changes (construction of a small dam and sections of concrete-lined canals). These irrigation changes are typical of small- and medium-scale irrigation. It illustrates several of the key factors involved in maintaining agrobiodiversity under irrigation.

Such maintenance of agrobiodiversity is a contrast to the loss and local elimination of agrobiodiversity that often has been assumed as inherent in irrigation development (e.g., under the “big dam” projects of the Green Revolution). By contrast, the shift to small- and medium-scale irrigation and associated new models of water resource management and landscape development definitely do not necessarily ensure the opposite outcome (continued high-agrobiodiversity farm production). Still the increase of this latter scenario does contain the possibility of *in situ* conservation under certain key conditions, as detailed in my study. As a result it is important to design landscape-based analysis of the key conditions that determine whether there is continued high-agrobiodiversity production under water development, since these conditions are ones that would enable *in situ* conservation. My study offers new insights in exploring the role, and identifying and examining the specific key social–ecological conditions and resilience, of agrobiodiversity in tropical mountain landscapes under irrigation development.

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Section V

Uses of Biodiversity and New and Future Domestications

Patrick McGuire and Calvin Qualset

In previous sections, we have learned of new techniques to investigate prehistoric domestications of crops and livestock, new hypotheses of domestication and spread of crops and livestock in human cultures, and the genetic basis for domestication. However, domestication is not only a process of the past. In spite of the fact that currently a very limited number of plant and animal domesticates contribute to the world's sustenance, new domestications are taking place and given what humans now know about the process, there are opportunities for new domestications that should be pursued.

The number of plant species that humans have made use of is huge. One estimate is that 75,000 angiosperm species are edible; 7,000 of these have been used by humans as food sources (Myers 1983). A more recent review puts it as 4,079 food species (Procheş *et al.* 2008), still a strong contrast to the few cultivated species that predominate today. However, Leakey (Chapter 22) makes the case that domestication is not a relict process of the past but should be deployed anew in many different situations with different indigenous crops. The focus is on tree crops and he clearly explains for each of the several examples just what traits and biological parameters should be featured, where the diversity exists for those traits, how to involve the participation of the potential growers and users of the crops in the process, and what are the potential markets and benefits of the crop. The arena for his examples is West Africa. The challenges of a sustainable agriculture in developing countries are compounded with the increasing uncertainties of a changing climate. The vision for the role of these new crops is that they would involve local participation in the process of their development, can augment the local economies, and could enhance the interface between agriculture production areas and the natural environment and its services.

The acceptance of any crop into ecosystems or cropping systems where it has not been previously found involves interplay of not only biological factors of adaptation and competition, but also societal preferences, political decisions, and economic incentives and disincentives. The relatively recent history of the addition

of the wine grape (*Vitis vinifera*) to California agriculture exemplifies the interaction of all these factors. [Chapter 23](#) by Lapsley sets out the biological, economic, and social challenges that wine grape production has met and overcome to become an iconic crop for California. The path from the production of sacramental wine in the early Spanish colonial days to today's staggering diversity of types and qualities and international prominence was not one of steady growth and improvement. Booms and busts have been the norm that Dr Lapsley's chapter documents and explains.

Full domestication is not a requirement for a species to be subject to extensive human use and exploitation for food and fiber. In fact, many such widely used taxa are only evident to humans by their activity or productivity in interaction with plants and animals more normally considered as food or food producers, not by any visible or tangible contact by humans with the organism itself. Bamforth in [Chapter 24](#) documents, with examples, the wide range of yeasts, mold, fungi, and bacteria utilized in fermentation processes acting on fruits, grains, and milk. Tables document the taxonomic diversity of these organisms, identify genetic stock collections, list the diverse uses made of micro-organisms, and, in one specific case, present the diversity of sources where different species of *Saccharomyces* have been found.

Pollinators represent another critical group of species, like yeasts and bacteria, not necessarily domesticated, but critical components of agroecosystems and necessary partners for the productivity of many crops. In [Chapter 25](#), Thorp emphasizes the role pollinators play for many California crops, the tenuous situation resulting for crops that depend on a single pollinator, when that pollinator, the honey bee, is threatened by disease and disorder, and the potential for widening the scope for what is considered as adequate pollinators to include more native pollinators. The conclusion is another demonstration of the value of managing biodiversity for human ends.

In [Chapter 26](#), Hedgecock discusses the many efforts at domestication of aquatic species that are on-going today and argues that it should be taking place more widely, given the decline of capture fisheries and increasing human dependence on aquatic food sources. He contrasts the historical perceptions (still held by many) of aquatic species with large populations and unlimited reproductive potential with the increasing evidence of very small effective breeding populations, extremely variable reproductive fitness from one individual to another, and the extremely high environmental variability tempering potential reproductive success. He argues that for many species the potential for genetic gain by crossbreeding is high; hybrid vigor can be as marked as in maize, for example. Conservation of aquatic diversity, within species and at the species level, must be achieved in a very different way from conservation of typical plant and terrestrial animal diversity. Conservation strategies will necessarily have to involve conservation of natural biodiversity broadly in the aquatic ecosystems. Success in utilizing while conserving and restoring will depend on continued and increased research, and on science-based fisheries management policies.

In a new or ongoing domestication process, the direction is from a large degree of genetic diversity to a smaller amount as diversity is screened, evaluated, and selected. In some long-domesticated plants and animals, there is concern about the reverse: too little genetic diversity. An extreme example of this is provided in [Chapter 27](#) by Medrano. The dairy industry, not just in California, is dominated by a single breed of cow. In spite of the millions of Holsteins that exist, breeding programs are such that the effective breeding population numbers only in the hundreds of individuals. Genome technologies applied to breeding programs are providing a much more cost- and time-effective approach to monitoring inbreeding, choosing the most diverse acceptable parentage combinations, and continuing the productivity of the breed. The alternative until now had been laborious progeny screening and testing before parent selections, requiring many years.

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22 Participatory Domestication of Indigenous Fruit and Nut Trees: New Crops for Sustainable Agriculture in Developing Countries

Roger R.B. Leakey

Crop domestication has been limited to a very small proportion of some 250,000 plant species (0.04%). This equates to 0.5% of the 20,000 edible species (Leakey and Tomich 1999). The process of domestication in many of these species goes back thousands of years, for example, barley domestication started in the Neolithic Age, while fruits like oranges and apples go back about 3,000 years in China and central Asia respectively (Simmonds 1976). Against this background the domestication of tropical tree crops, such as mango and lychee, is very recent, probably only within the last century. Likewise, the concept of domesticating trees for timber and non-timber products in forestry emerged only within the last 30 to 40 years (Okafor 1980, 1983, Leakey *et al.* 1982, Leakey 1991). In 1992, a conference in Edinburgh recognized the need to domesticate the trees that have in the past provided poor people with their everyday needs for food, medicinal and other forest products (Leakey and Newton 1994a,b). At this conference, these species were described as “Cinderella species” because they have been overlooked by science and the “Green Revolution” (Leakey and Newton 1994c). The recent history of agroforestry tree domestication has been chronicled by Leakey *et al.* (2005a, 2007), and the products of these cultivated trees are now termed Agroforestry Tree Products (AFTPs) to distinguish them from the extractive resource of Non-timber Forest Products (NTFPs) (Simons and Leakey, 2004).

Agroforestry practices are especially numerous in the tropics and used by more than 1.2 billion people. They produce the products that are important for the livelihoods of millions of other people in developing countries. The area under agroforestry world-wide has not been determined, but probably exceeds 100 million hectares. Like organic farming, conservation agriculture and ecoagriculture, agroforestry addresses soil fertility management issues for the rehabilitation of degraded farming systems; loss of biodiversity above and below ground; carbon sequestration; and soil and watershed protection. In addition, agroforestry provides: (i) useful and marketable tree products for income generation, fuel, food

and nutritional security/health and the enhancement of local livelihoods (Leakey *et al.* 2005d); (ii) functioning agroecosystems akin to natural woodlands and forests (Leakey 1996); (iii) linkages with culture through the food and other products of traditional importance to local people (Wynberg *et al.* 2003). On the “down-side”, trees are competitive with crops (Cooper *et al.* 1996) and the net benefits of agroforestry can be slow to materialize due to the longevity of trees. However, techniques exist to speed-up the benefit flows.

According to Diamond (1997), species have been domesticated as the precursor to the development of settled, politically centralized, socially stratified, economically complex, and technologically innovative societies; while P. Gepts (pers. comm.) says that domestication is stimulated when demand exceeds supply. The latter would explain the relatively recent need to domesticate tree crops from wild forest species in the tropics, as deforestation has increased in proportion to population growth. Interestingly, some poor smallholder farmers have reacted to deforestation by starting to select useful trees for growth within their farms (Leakey *et al.* 2004, Leakey, 2005). These farmers can probably be said to be practicing “commensal” domestication (cf. Zeder, Chapter 9, this volume) as they have retained natural seedlings in their fields and home gardens and cut down those that do not have desirable characteristics when they clear land for other crops. Second, they also sow and disperse the seeds of the tastier fruits that they eat, close to the homestead. This approach is less scientific than the “direct” pathway to domestication that is now being taken by agroforesters who recognize that population growth and deforestation are potent forces in the downward spiral of poverty, hunger, malnutrition, and environmental degradation. One constraint to tree domestication is that they are notoriously difficult to domesticate because they are out-breeding. This means that gains in selected traits are on average small because of the wide range of intra-specific variation in the progeny arising from controlled pollinations. Additionally the long generation time of many trees (10–20 years), means that an individual geneticist does not produce many generations within his/her career. These problems can be overcome by a horticultural approach to domestication, using vegetative propagation to mass produce individual trees with superior characteristics. Until recently, however, trees have had the reputation of being very difficult to propagate by stem cuttings, and the alternative approaches of budding and grafting have other technical difficulties (graft incompatibility, dominance by the rootstock, etc.), as well as requiring some special skills. Nevertheless, perhaps the over-riding factor that constrained the “direct” approach to tree domestication has been the disinterest in products that did not appeal to “western” tastes. Consequently they were neither promoted by early European settlers, nor were they funded by the “Green Revolution”.

Against this background the 1992, Edinburgh conference (Leakey and Newton 1994c), recognized that “somehow a way has to be found to make the land more productive and to rehabilitate degraded areas in a way which will diversify production, promote genetic conservation, enhance the development of sustainable land use and contribute to domestic, regional and international trade”. The

Table 22.1. Tree species being domesticated clonally that have potential as components of agroforestry systems

Species	Use	Reference
<i>Irvingia gabonensis</i> and <i>I. wombulu</i>	Kernels and fruits	Okafor 1980, Shiembo <i>et al.</i> 1996a, Atangana <i>et al.</i> 2001, 2002, Anegbah <i>et al.</i> 2003, Leakey <i>et al.</i> 2005a
<i>Dacryodes edulis</i>	Fruits and oils	Okafor 1983, Kengue <i>et al.</i> 2002, Tchoundjeu <i>et al.</i> 2002b, Waruhiu <i>et al.</i> 2004, Anegbah <i>et al.</i> 2005
<i>Prunus africana</i>	Bark for medicinal products	Simons <i>et al.</i> 2000, Leakey 1997, Tchoundjeu <i>et al.</i> 2002a, Simons and Leakey 2004.
<i>Pausinystalia johimbe</i>	Bark for medicinal products	Ngo Mpeck <i>et al.</i> 2003b, Tchoundjeu <i>et al.</i> 2004
<i>Ricinodendron</i> <i>heudelottii</i>	Kernels	Shiembo <i>et al.</i> 1997, Ngo Mpeck <i>et al.</i> 2003a
<i>Gnetum africanum</i>	Leafy vegetable	Shiembo <i>et al.</i> 1996b, Mialoundama 1993.
<i>Barringtonia procera</i>	Nuts	Pauku 2005
<i>Inocarpus fagifer</i>	Nuts	Pauku 2005
<i>Santalum</i> <i>austrocaledonicum</i> and <i>S. lanceolatum</i>	Essential oils	Page <i>et al.</i> 2007a,b
<i>Canarium indicum</i>	Nuts	Nevenimo <i>et al.</i> 2007, Leakey <i>et al.</i> 2008
<i>Sclerocarya birrea</i>	Fruits and nuts	Leakey <i>et al.</i> 2005b,c, Leakey 2005
<i>Triplochiton scleroxylon</i>	Timber	Longman and Leakey 1995, Ladipo <i>et al.</i> 1991a,b, 1992
<i>Chlorophora excelsa</i>	Timber	Ofori <i>et al.</i> 1996a,b, 1997
<i>Swietenia macrophylla</i> and <i>S. mahagoni</i>	Timber	Newton <i>et al.</i> 1993

conference also recognized the need to know how to grow the “Cinderella” trees wanted by farmers; how to make them more desirable and productive so that they could satisfy the farmers’ needs and even promoting a surplus which could be sold to urban populations. It was hoped that this conference would “inspire fairy godmothers, particularly policy-makers and donors, to mobilise their glass carriages and get Cinderella to the ball”. Now, 17 years later, this chapter can report that many Cinderella species are being domesticated all around the world (Table 22.1), thanks to the efforts of a growing number of people.

1

The road to “The Ball”

Harlan (1975) said that crop domestication is human-induced change in the genetics of a plant to conform to human desires and agroecosystems, culminating in the

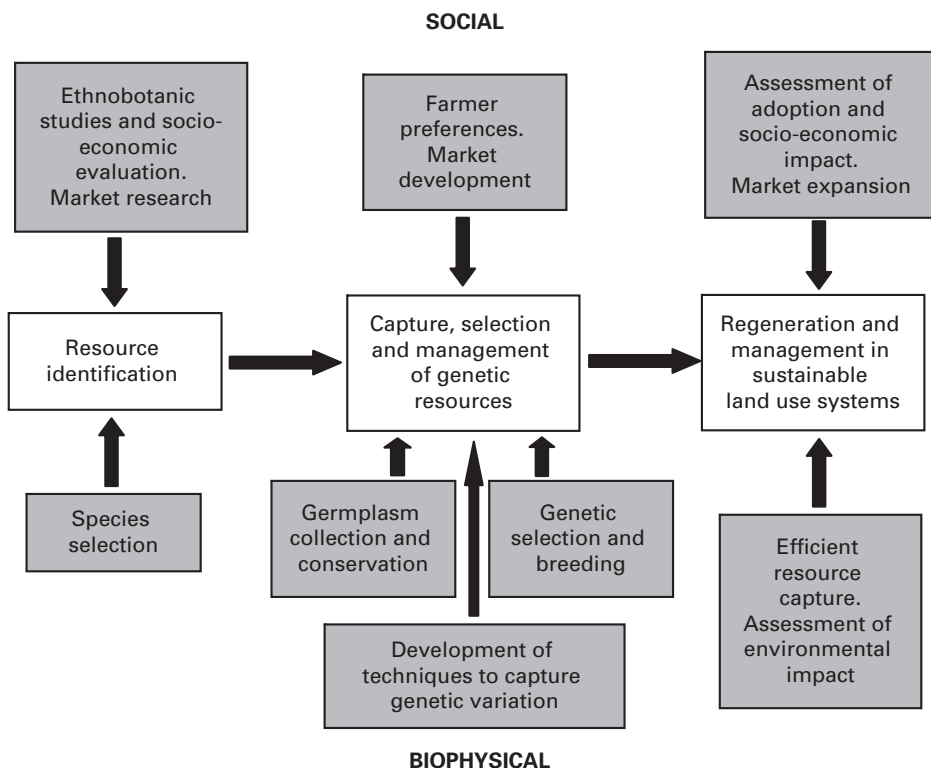


Figure 22.1. Definition of domestication (after Leakey and Newton 1994a,b).

plant's loss of its ability to survive in natural ecosystems. In these terms Cinderella species are still wild, as they are alive and well in natural systems. Perhaps in the future, as our agricultural systems become more sustainable and multifunctional (Leakey *et al.* 2009), domesticates will no longer need to lose touch with their natural ecosystems. The development of multifunctional agriculture has recently been suggested by International Assessment of Agricultural Knowledge, Science and Technology for Development (IAASTD) to replace the current exploitative forms of agriculture (Kiers *et al.* 2008, McIntyre *et al.* 2009).

The definition of domestication used for agroforestry trees (Leakey and Newton, 2004 a,b) encompasses the socio-economic and biophysical processes involved in the identification and characterisation of germplasm resources; the capture, selection, and management of genetic resources; and the regeneration and sustainable cultivation of the species in managed ecosystems (Figure 22.1). This definition therefore stresses that domesticates will be compatible with sustainable land use systems and have beneficial socio-economic and environmental impacts. Consequently, the domestication of agroforestry trees is an incentive to promote sustainable agriculture through diversification with species which generate income, improve diets and health, meet domestic needs, and restore functional

agroecosystems; as well as empowering local communities. In agroforestry, domestication is an ongoing process that is never finished. However, otherwise, the concept is similar to that of Harlan and others.

Progress in developing the techniques and strategies for the domestication of agroforestry trees is most advanced in humid West Africa, where the concepts were first developed (Simons 1996). Now, led by the World Agroforestry Centre (formerly the International Centre for Research in Agroforestry), the domestication of agroforestry trees is a world-wide initiative that is being implemented by many different players, in many different temperate and tropical environments, from rainforest to semi-arid desert.

Part of the solution to agricultural sustainability foreseen by IAASTD is for farming to provide the livelihood needs of the local communities in every region around the tropics through the domestication of indigenous species that can become new crops that generate income and enhance food nutritional security. Fortunately, there are local and regional markets for these culturally important species which also provide dietary micro-nutrients that boost immunity to diseases like AIDS.

2 Domestication strategies

First, for the purpose of efficiency and speed, the domestication strategy adopted by agroforestry has been a clonal one, based on horticultural techniques of vegetative propagation (Leakey 2004), applied in a very robust and low-tech manner (Leakey *et al.* 1990) so as to be appropriate for implementation in remote areas of tropical countries which lack reliable supplies of running water or electricity. Second, to benefit the target population of poor smallholder farmers, the strategy is based on Participatory Approaches to both decision-making and implementation (Tchoundjeu *et al.* 1998, Leakey *et al.* 2003). This foundation in participatory processes ensures that domestication is a *farmer-driven* process that also has an eye on the local market to ensure that farmers will be able to sell their products (Simons 1996, Leakey and Simons 1998, Simons and Leakey 2004).

Vegetative propagation is a uniquely powerful means of capturing existing genetic traits and fixing them so that they can be used as the basis of a genetic “variety” or “cultivar”. The advantage of using clonal propagules outweighs those of seedlings when the products are valuable; when the tree has a long generation time and when the seeds are scarce or difficult to keep in storage (Leakey and Akinnifesi 2008). The consequent uniformity in the crop is advantageous in terms of maximizing quality, meeting market specifications, and increasing productivity, but it also increases the risks of pest and disease problems, consequently, risk aversion through the diversification of the clonal production population is a crucial component of the strategies used.

A participatory approach to the domestication of agroforestry trees has been adopted in order to address the need to empower poor, smallholder farmers to be

self-sufficient and to raise themselves out of poverty, malnutrition, and hunger through enhanced livelihoods, and food and nutritional security. To initiate this participatory approach and ensure that farmers were both interested and keen to be involved, the programme started with a participatory exercise in priority setting, in which farmers listed their preferred species for domestication (Franzel *et al.* 1996). Interestingly, almost everywhere in the world where this has been done, farmers have selected indigenous fruits and nuts as their top priority. This is because these traditionally important products are no longer readily available in the wild and they are important domestically to rural people because of their cultural and nutritional value, as well as their familiarity and position in local markets. These same values probably also explain why the participatory domestication of these species is being so rapidly adopted by rural communities (Tchoundjeu *et al.* 2006). After about ten years the number of engaged communities had grown from two pilot villages in Cameroon to 35 villages in southern Cameroon (about 2,500 farmers), 11 villages in Nigeria (about 2,000 farmers), three villages in Gabon (about 800 farmers), and two villages in Equatorial Guinea (about 500 farmers). Now in 2008, the number of villages in Cameroon exceeds 100 (Z. Tchoundjeu, pers. comm.).

The strategy is also important because it conforms to the Convention on Biological Diversity (Tchoundjeu *et al.* 1998, Leakey *et al.* 2003, Simons and Leakey 2004), by recognizing the rights of local people to their indigenous knowledge and traditional use of native plant species. Protection of the farmers' intellectual property is needed to ensure that participatory domestication by local farmers can be recognized as a good model of Biodiscovery; an alternative to Biopiracy by expatriate or local entrepreneurs. However, until global negotiations create an effective means of protecting the intellectual property of farmers, they remain at risk of being exploited.

This strategy involves the maintenance and use of three interlinked populations (Figure 22.2):

- Gene Resource Population, for genetic conservation
- Selection Population, for the development of improved cultivars, and
- Production Population, for farmers to plant and grow.

The strategy is equally appropriate for the domestication of species producing fruits and nuts; medicinal products; leafy vegetable and animal fodder; timber and wood; and extractives like essential oils, resins, etc. (Table 22.1).

3 Domestication processes

A fundamental requirement of the clonal approach to domestication is a good understanding of the intraspecific variation in all traits of importance for selection and improvement. Consequently, quantitative studies have been made of the tree-to-tree variation in a range of fruit and nut traits to determine the

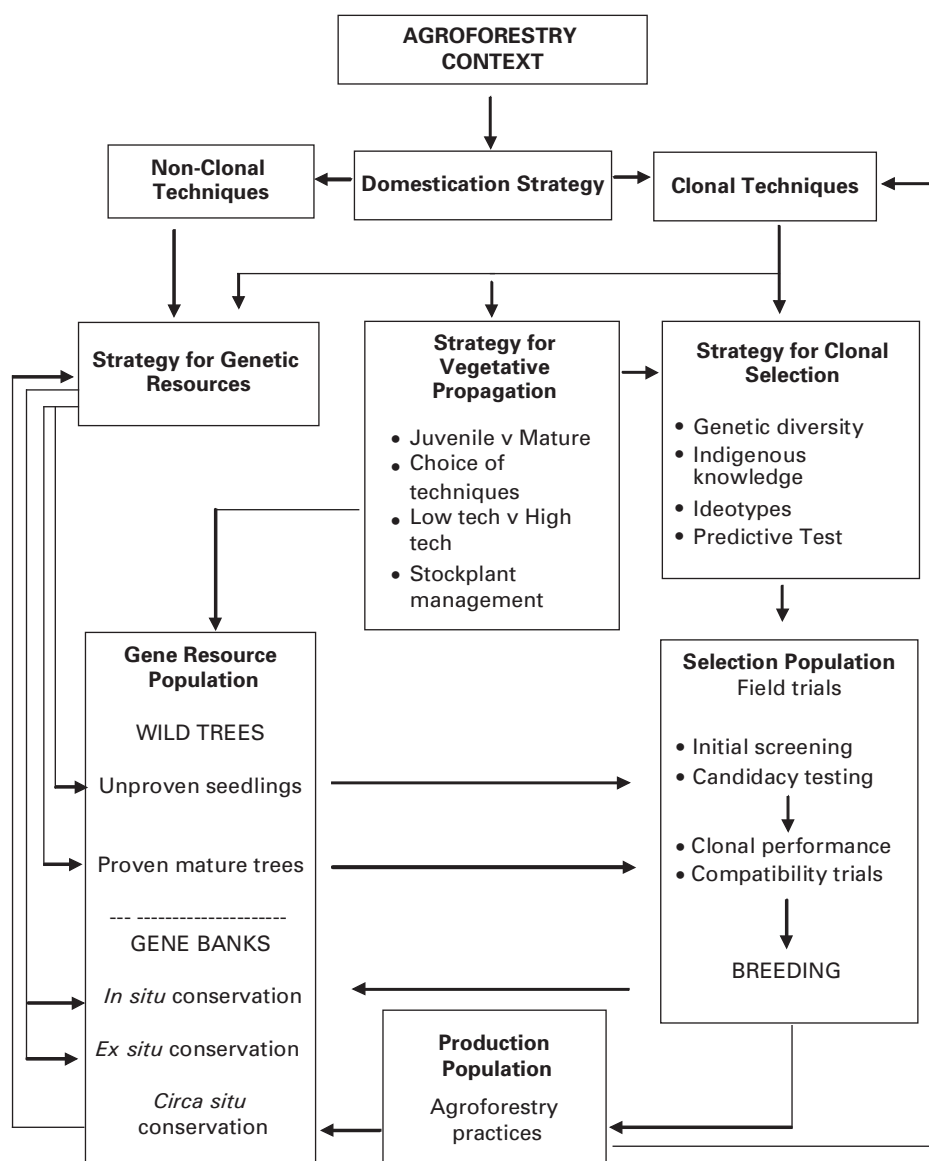


Figure 22.2. Domestication strategy for agroforestry trees (after Leakey and Akinnifesi 2008).

potential for highly productive and qualitatively superior cultivars with a high Harvest Index (e.g. Atangana *et al.* 2001, 2002, Anegbah *et al.* 2003, 2005, Leakey *et al.* 2002, Waruhiu *et al.* 2004, Ngo Mpeck *et al.* 2003a, Leakey *et al.* 2005b,c, Page *et al.* 2007a,b, Leakey *et al.* 2008). This information is needed in order to identify the elite trees with the desirable combinations of different traits that would be appreciated by different markets (e.g., edible fruits, edible nuts,

nuts for food oil, nuts for cosmetic oils, or fruits and nuts for medicinal products). The practical approach is to seek trees that have particular, market-oriented, trait combinations – such as big, sweet fruits (even seedlessness) for the fresh fruit market (a fruit ideotype); big, easily extracted kernels for the kernel market (kernel ideotype), etc. The latter can then be sub-divided into those meeting the demands of different markets (Leakey and Page 2006), such as food thickening agents conferring drawability and viscosity (Leakey *et al.* 2005a), or other products, such as pectins or oils for food or cosmetic industries (Kalenda *et al.* 2002, Kapseu *et al.* 2002, Leakey *et al.* 2005b). One of the key findings of these characterization studies is that each trait shows very considerable and continuous variation from low to high values. Interestingly, this is greatest at the village level, while the variation between villages is only modest. Importantly, it is also found that high values of one trait are not necessarily associated with high values of another trait: thus large fruits are not necessarily sweet fruits, and do not necessarily contain large nuts or kernels. Consequently the more trees that are examined the greater are the opportunities for creating exciting new cultivars.

A start has been made to look at the genetic variability in nutritive value or sensory analysis in any of the new AFTP-producing crops. Kengni *et al.* (2001) have made a preliminary examination of the variability in flavor, taste, and aroma in samples of *Dacryodes edulis*, while a similar preliminary analysis of *Sclerocarya birrea* fruits has identified considerable tree-to-tree variation in protein and vitamin C (Thiong'o *et al.* 2002). Similarly, preliminary studies have been done in *Canarium indicum* to evaluate tree-to-tree variation in fatty acid profiles, protein and vitamin E, anti-oxidant activity, and phenolic content (Leakey *et al.* 2008). Interestingly, the latter study also identified very considerable tree-to-tree variation in the anti-inflammatory property of kernel oil between just ten trees, illustrating the very real opportunity to develop cultivars for medicinal properties. Other evidence of tree-to-tree variation in medicinal value has been recorded in the major sterol component, B-sitosterol, from the bark of *Prunus africana*, which is of importance for the treatment of Benign Prostatic Hyperplasia (Simons and Leakey, 2004). This variability in nutritional quality and medicinal properties is likely to affect the potential for different markets, so there is an urgent need for agroforesters to work closely with the food, nutraceutical, and pharmaceutical industries to optimize the domestication/commercialization partnerships (Leakey 1999). One aspect of the potential health benefits of agroforestry is the fortification of the immune systems of HIV/AIDS sufferers through the selection of especially nutritious cultivars of indigenous fruits and nuts (Barany *et al.* 2001, 2003); this is something that requires further investigation as an output from agroforestry (Villarreal *et al.* 2006).

In addition to these qualitative traits there is also the opportunity for cultivars to capture variation in quantitative traits and in phenology, such as yield, seasonality and regularity of production, reproductive biology, and reduction of susceptibility to pests and diseases, which can reduce productivity or quality (Kengue

et al. 2002). High yield is obviously a desirable trait, but in the early stages of domestication it may be even more important economically, nutritionally, etc., to expand the fruiting season from 2–4 to 6–8, or even 12 months. Emerging evidence suggest that in many species there are rare individuals that flower and fruit outside the main season, so this possibility is not just wishful thinking.

Having identified which are the elite trees worthy of becoming cultivars, they are propagated vegetatively to capture the specific combination of genetic traits as a clone (Leakey *et al.* 1990, Leakey 1991). To ensure that optimal use of the genetic resource is achieved, the clonal approach is integrated with others to ensure that a wise genetic improvement strategy is adopted (Leakey and Akinnifesi, 2008). The use of vegetative propagation techniques to capture the tree-to-tree variation is now relatively simple and well understood (Leakey 1985, 2004, Leakey *et al.* 1990 1996, Mudge and Brennan 1999), with high multiplication rates, for almost all tree species, although the numbers of people with the appropriate skills may be a constraint on its widespread application in the future (Simons and Leakey, 2004). Typically, the techniques of grafting, budding, and air-layering (marcotting) are used to capture superior fruit trees and to multiply them as cultivars. This is because mature tissues with the capacity to flower and fruit can only be propagated by cuttings with great difficulty (low multiplication rates) (Leakey, 2004). Propagation by cuttings is, however, the preferred option for participatory domestication in village nurseries (Mialoundama *et al.* 2002, Tchoundjeu *et al.* 2002a), and ways have to be found to overcome the difficulty of propagating mature shoots with the capacity to flower and fruit. Circumventing this problem is most easily achieved by capturing the genotype as a graft or rooted marcot, and then by good nursery management, enhancing the rooting ability of the resulting stock-plant once it is severed from the tree and on its own roots.

4 Retention and protection of genetic diversity

Typically only the best plants are brought into domestication programs, so domestication is generally considered to reduce the genetic diversity of the species being domesticated; creating the so-called “domestication bottleneck”. This is probably true in situations where the domesticated plant replaces or dominates the wild origin, but is probably not the case at the current level of domestication of agroforestry trees. So, for example, in most of the trees currently being domesticated there is still a robust wild population. Evidence from molecular studies of *Barringtonia procera* in the Solomon Islands (Pauku, 2005) found that the trees with the largest kernels were found in many different populations and so were not closely related. Thus selected cultivars produced by different communities will all have large kernels but they will be genetically diverse in all the unselected traits, such as pest and disease resistance, etc. This population variation is another advantage of a participatory domestication strategy implemented independently in different villages (Leakey *et al.* 2003).

Modern molecular techniques are useful in the development of a wise strategy for the maintenance of genetic diversity, as within the geographic range of a particular species they can be used to identify the “hot-spots” of intraspecific diversity (e.g., Lowe *et al.* 1998, 2000), places that should if possible be protected for *in situ* genetic conservation, or be the source of germplasm collections if *ex situ* conservation is required.

5 Social, economic, and environmental benefits of domestication

Crop domestication has been credited with being one of the major stimulants of agricultural development and hence the diversification of civil society and economic development, and even the evolution of civilization (Diamond 1997). This illustrates the close linkage between domestication and the commercialization of the products. Recognizing this linkage and deliberately promoting the parallel development of domestication and commercialization is a very important part of the domestication strategy for agroforestry trees (Leakey 1999, Leakey and Akinnifesi, 2008, Bunt and Leakey, 2008). In west and central Africa, a number of indigenous fruits and nuts, mostly gathered from farm trees, contribute to regional trade (Ndoye *et al.* 1997). In Cameroon, the annual trade of the products of five key species has been valued at US\$7.5 million, of which exports generate US\$2.5 million (Awono *et al.* 2002). Perhaps because of this trade, evidence is accumulating that AFTPs do contribute significantly to household income (Gockowski *et al.* 1997) and to household welfare (Schreckenber *et al.* 2002, Degrande *et al.* 2006).

In terms of social benefits, women, who are the main retailers of NTFPs (Awono *et al.* 2002), are often the beneficiaries of this trade and they have especially indicated their interest in marketing *D. edulis* fruits because the fruiting season coincides with the time to pay school fees and to buy school uniforms (Schreckenber *et al.* 2002). The role of women in trade and marketing of AFTPs is being enhanced by domestication, and it is hoped that children will also benefit, not only from improved nutrition, but by greater access to education. Similar trends are emerging in southern Africa, where indigenous fruits have relatively new local and international markets (Brigham *et al.* 1996, Shackleton *et al.* 2000, 2002, 2003b). Because the production and trading of AFTPs are based on traditional lifestyles, it is relatively easy for new producers to enter into production and trade with minimal skills and low capital requirement, and with little need for external inputs. Together these things make this approach to intensifying production and enhancing household livelihoods very easy and adoptable by poor people.

In many cases the successful commercialisation of AFTPs is dependent on domestication to improve quality and product uniformity and reduce the seasonality of production, as initiatives to develop markets for new products frequently fail when supply does not meet the demand. This is especially problematic if the product is derived from many small growers, with minimal quality control.

6 Integrating domesticates into the cropping system

6.1 Agroforestry, agroecology, and the role of biodiversity in sustainability

Agroforestry is defined as “*a dynamic, ecologically-based natural resources management system that, through the integration of trees into agricultural systems and landscapes, diversifies and increases production, while simultaneously promoting social, economic and environmental benefits for land users*” and involves the development of an agroecological succession akin to natural succession in woodland/forest ecosystems (Leakey 1996). Through domestication the “planned biodiversity” planted by the farmer includes a range of species producing high-quality marketable products from indigenous tree species. These trees also increase the numbers of niches for the “unplanned biodiversity” that is essential for the effective function of the agroecosystem: pest and disease control; pollination; nutrient, carbon and water cycling; and so on. However, currently it is not known how many species (or ecological functional groups) are required to ensure sustainable production. The acquisition of this knowledge is one of the scientific challenges of our time. To try to acquire this knowledge, studies are in progress in Brazil and Vietnam to elucidate some of the ecological interactions between cocoa, shade trees, and companion crops (Leakey 2011). Specifically, both these studies seek to examine the relationships in mixed species cocoa agroforests between spacing, microclimate, the planned and unplanned biological diversity, the incidence of pests and diseases in cocoa, and the overall production and economic returns from cocoa and the other companion trees. Both these experiments are also examining how a range of indigenous companion crops producing AFTPs can additionally provide income generation and livelihood benefits.

6.2 Rehabilitation of degraded land together for economic, social, and environmental benefits

In many domesticated crops, the market demand for the product has promoted large-scale monocultural production systems that frequently have been the cause of environmental degradation through deforestation, soil erosion, nutrient mining, and loss of biodiversity. In the developing tropics, this degradation has typically resulted in the “poverty trap” for small-scale producers who are unable to purchase inputs. Agroforestry aims to rehabilitate degraded land and so be beneficial to the environment and beneficial to the poor farmer. In this case domestication can perhaps be part of the solution, rather than a contributor to the problem, by helping to be the stimulus to a more sustainable farming system. Specifically, the domestication of indigenous trees is one of the steps in addressing the “yield gap” – the difference between potential yield and actual yield. In African maize production, this gap is the result of land clearance, exhausted soil health and fertility, and the “poverty trap”, which makes chemical fertilizers unavailable. Through improved land husbandry, agroforestry offers an integrated

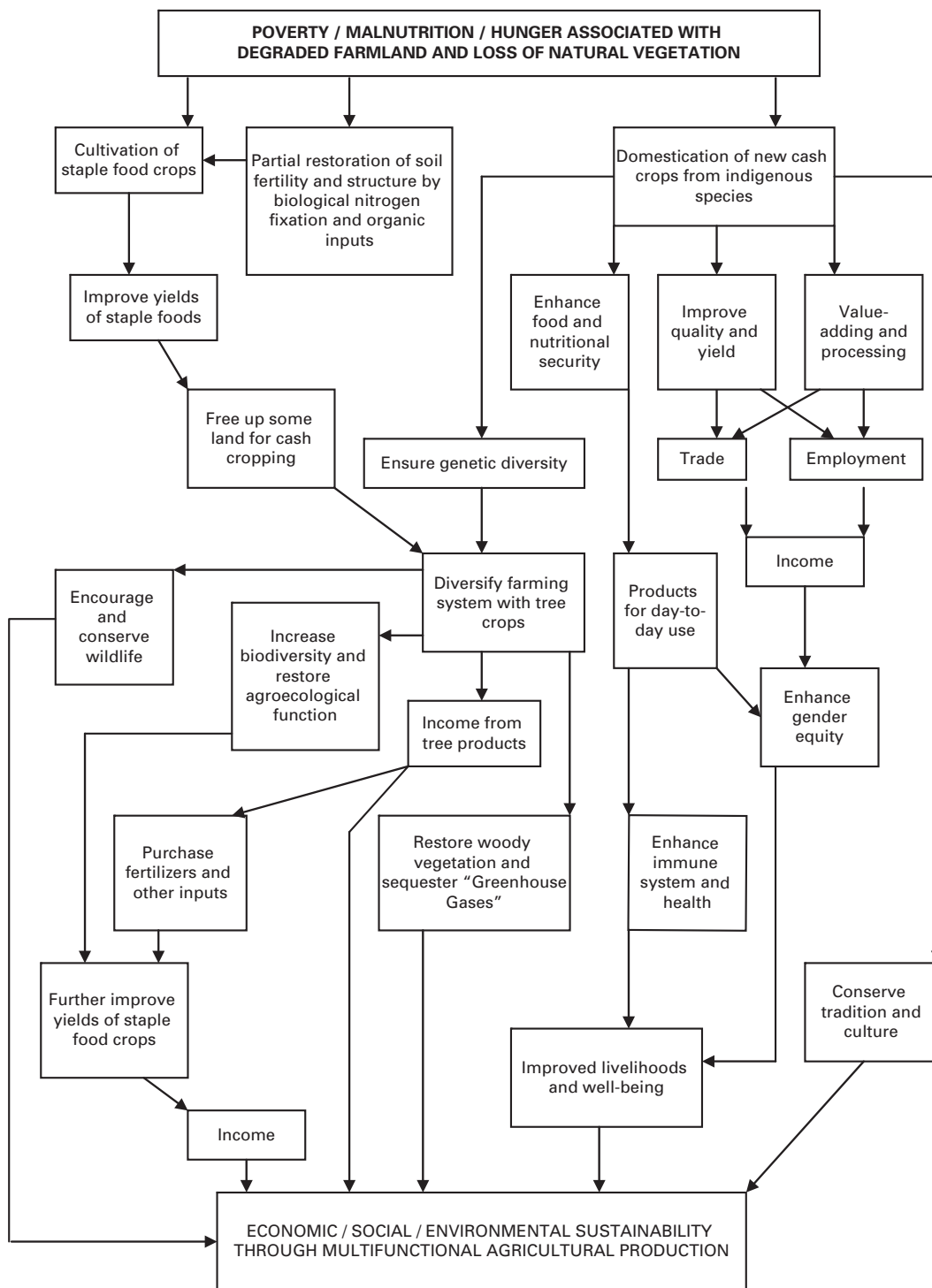


Figure 22.3. Agroforestry approach to closing the Yield Gap.

three-step approach to bringing actual yield closer to potential yield (Figure 22.3), which rebuilds natural soil fertility and health and, through enterprise diversification with perennial cash crops, generates income.

Step 1. Adopt agroforestry technologies such as two-year “Improved fallows” or “Relay cropping” with nitrogen-fixing shrubs that improve maize yields from around 1 tonne per hectare to about 4–5 tonnes per hectare (Cooper *et al.* 1996). This allows farmers to reduce the area of their holdings under maize and so allow them to grow other crops, perhaps cash crops which would generate income. There is also evidence that this agroecological approach to land rehabilitation also increases yield by reducing pest and disease problems (Gatsby Charitable Foundation 2005). This is achieved by the introduction of nature’s checks and balances into the farming system, such as bait plants for pests and diseases, as well as introducing plants that deter pests and support pest predators.

Step 2. Adopt the Participatory Domestication of indigenous fruit, nut and medicinal trees so that new, locally important cash crops are rapidly developed as a source of income and products of day-to-day domestic importance, that also are rich in micro-nutrients, empower women, and maintain culture and traditions (Leakey *et al.* 2003, 2005a). Sale of these products would allow modest use of, and so potentially the increase of, maize yields to up to 8–10 t/ha in this more resilient agroecosystem. Consequently the area under maize could be reduced further to allow more cash cropping.

Step 3. Commercialization of AFTPs to expand the market opportunities should involve in-country processing and value-adding of the new products, so creating off-farm employment and business opportunities. In this way, local society can be diversified so that some community members can move out of agricultural production and create wealth. Evidence suggests that this commercialization can be done in ways that maintain local culture and tradition (Wynberg *et al.* 2003).

Life, however, is a complex and highly interactive web of social, economic, and environmental factors; sometimes the outcome of actions are counter-intuitive, and so fraught with danger of making serious errors of judgement. To reduce the risk of such errors it is important to engage with local people in participatory information-gathering and decision-making, as well as working with scientists from other disciplines. One such risk is that the domestication of agroforestry trees could be so successful that an entrepreneur or company decides to develop monocultural plantations, rather than supporting polycultural agroforests. Worse still perhaps, such plantations might be developed in an overseas location with a similar climate and better access to markets. This could undermine the whole purpose of developing the new crops as a means to enhancing food security, health, income generation, and environmental rehabilitation. Hopefully, the potential benefits from domestication will outweigh the risks and fortunately, there is a move by a few multinational companies to work with and in support of local communities.

One multidisciplinary, multinational study has assessed the risks that the domestication and commercialization of agroforestry trees will result in both “Winners and Losers”. This study examined the likely impacts of commercialization on the five forms of Livelihood Capital (Human, Social, Financial, Natural, and Physical). The conclusion from this study was that positive outcomes can be maximized if the importance of community involvement is appreciated by external players and if the communities themselves work together and use their own strengths to manage and use their resources effectively. This provides encouragement and some endorsement that the approach being developed for the participatory domestication of agroforestry trees is appropriate. Nevertheless, to ensure the farmers engaged in participatory domestication are Winners, there is the need to resolve the current difficulties facing farmers wishing to protect their rights to the cultivars that they are producing (Leakey *et al.* 2003, Sullivan and O’Regan, 2003, Wynberg *et al.* 2003).

7 Domestication as a catalyst to multifunctionality

7.1 IAASTD and new strategies for rural development

Land degradation is one of the most serious problems facing agriculture as it affects 2,000 million hectares (38% of the world’s cropland). This is especially serious as there is no longer the option of expanding farming systems into natural forests and woodlands. To rehabilitate degraded land and restore sustainability requires soil fertility replenishment, diversification at the plot and landscape level, and perennial vegetation to provide environmental services and increase the number of niches in the agroecosystem. Domestication has an important role in addressing these issues because, through diversification with cash crops, the farming system can enhance nutrient cycling, produce marketable products to meet the everyday needs of local people, and help to counter climate change. The “Green Revolution” promoted intensive production of high-yielding staple food crops on land cleared of much of its natural vegetation. To be productive for more than a few years these crops required inputs of fertilizers, pesticides, and often irrigation. Different problems arise. In intensive industrialized farming, fertilizer and pesticide use is often excessive and environmentally damaging while in many parts of the developing world poor farmers do not have sufficient access to these inputs, AKST and other resources. In both cases other ways have to be found to maintain and restore soil fertility and maintain sustainable production, such as low-input resource-conserving technologies based on integrated management systems and an understanding of agroecology and soil science (e.g., agroforestry, conservation agriculture, ecoagriculture, organic agriculture, and permaculture) which minimize the need for high inputs. These low-input systems are also socially relevant, pro-poor, approaches to agriculture that can also build social capital at community and landscape levels and are especially relevant to smallholder

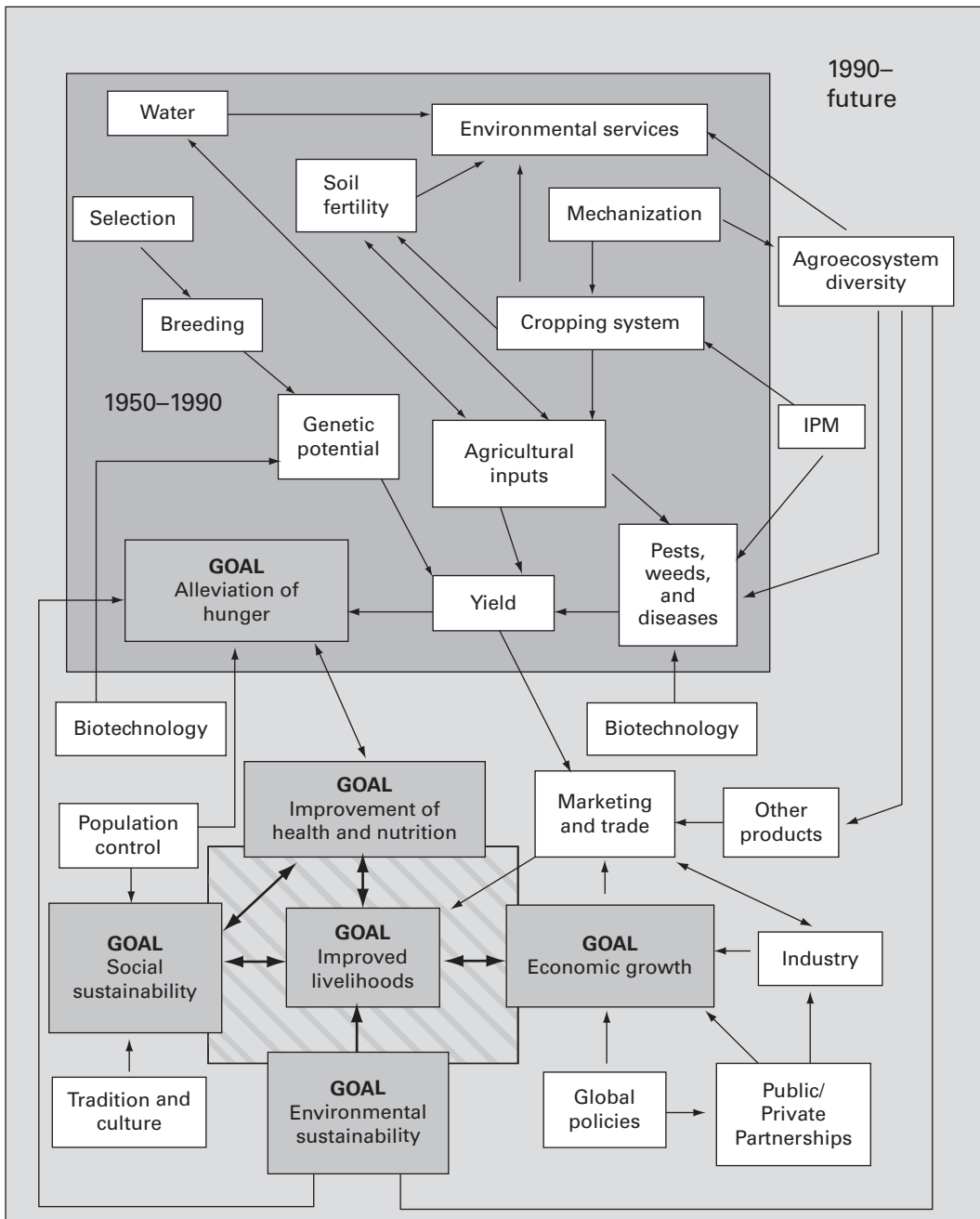


Figure 22.4. Evolution of agriculture and the IAASTD Goals.

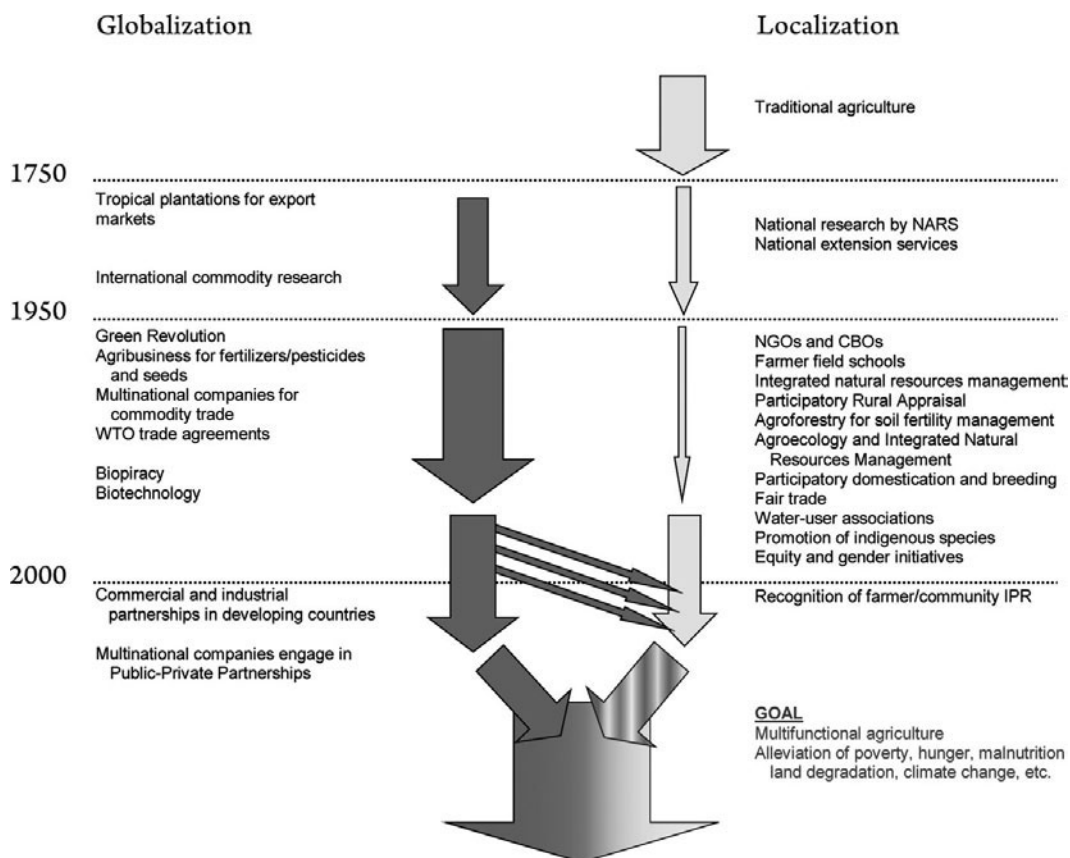


Figure 22.5. The globalization and localization pathways to rural development.

agriculture in the tropics. Thus they promote multifunctional agriculture, whose goals are to reduce hunger, improve nutrition and health, improve social and environmental sustainability, enhance farmer livelihoods, and promote economic growth (Figure 22.4).

Participatory domestication of agroforestry trees is aimed at empowering local communities, promoting food self-sufficiency, generating income and employment, and enhancing nutritional benefits. Consequently, this approach brings together agricultural science and technology with traditional knowledge at the local level as an integrated package capable of helping to meet IAASTD goals and so help farmers to be self-sufficient and support their families on an area of less than 5 ha.

7.2 Localization and the role of Public–Private Partnerships

Increasingly over the past few centuries, the concept of “Globalization” has dominated agricultural research and development, as well as international trade. This has been at the expense of Localization: the grassroots pathway to development relevant to local communities (Figure 22.5). However, in the past decade

there have been some initiatives to redress the balance between Globalization and Localization, so that both pathways can jointly play their optimal role. One of these is agroforestry, which involves scaling up the more durable and sustainable aspects of community-oriented rural development. The scaling up of all the many small and often rather specific positive impacts of local AKST held by farmers and traders helps to rebuild natural and social capital in the poorest countries. Interestingly, a small number of multinational companies are also becoming involved by increasing investment in the poorest countries (Mitschein and Miranda 1998, Panik 1998, Shapiro and Rosenquist, 2004, Attipoe *et al.* 2006), by addressing structural causes of poverty and environmental damage through agroforestry with locally available resources (skills, knowledge, leadership, etc). These new and exciting Public–Private partnerships involve diverse stakeholder groups at the local level, especially the farmers, to support sustainable production, tree domestication, and in-country processing and value-adding of agroforestry products.

8 Conclusions

It has been shown that the domestication of indigenous trees for integration into farming systems through agroforestry has positive impacts on the economic, social, and environmental sustainability of smallholder farming systems, especially in Africa. Much remains to be done to expand this approach to the rehabilitation of degraded farmland and the improvement of agricultural production, both of which current trap billions of people in poverty, malnutrition, and hunger. Consequently, there is a massive need for geneticists to engage in a new wave of domestication, at least as great as the First Wave which culminated in the Green Revolution and focused on staple food crops. We need a Second Wave of domestication focused on the species that provide the everyday needs of smallholder tropical farmers, and less on the needs of the First World. Through agroforestry, equally large impacts on global food production could be achieved, rehabilitating degraded land, closing the “yield gap”, and filling many agroecological niches with species producing a wide range of marketable and domestically useful products, including shade-adapted species and cultivars. In this way, there can be economic, social, and environmental benefit flows from agriculture of importance for the future of humankind, as in addition to increasing total factor productivity, trees have positive impacts on the environment and help to mitigate climate change.

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23 The Introduction and Dispersal of *Vitis vinifera* into California: A Case Study of the Interaction of People, Plants, Economics, and Environment

James Lapsley

The USA was the fourth largest producer of wine in 2007, behind only France, Italy, and Spain (Castellucci 2008). Since, with just over 523,000 acres of wine grapes (CASS 2008), California produces approximately 90% of all wine produced in the USA (USDA NASS 2009), that fourth-place spot essentially belongs to California. Because the wine grape (*Vitis vinifera*) is not native to California and was introduced into the state only in the late eighteenth century, the spread of vineyards across California in two and a half centuries represents an unusually successful partnership between humans and plants. The introduction of *V. vinifera* and the expansion of vineyards were not continuous processes, but rather were the result of boom periods, during which cultivars were introduced and new areas planted, generally followed by periods of decline, when vineyards were abandoned or converted to other crops. Although the initial impetus for each boom period was an increase in the price of wine, which enhanced winery and vineyard profitability, thus encouraging expansion, the specifics of each boom period differed, both in the type of grapes planted and the geographic areas developed. This brief history reviews the major periods of planting within California, examining the causes for the increased production, the locations developed, and the cultivars chosen.

Vitis vinifera is the principal species of the genus *Vitis* used for wine production. Derived from the wild *V. silvestris*, *V. vinifera* (literally “wine bearer” in Latin) is unusual in both the size and high sugar concentration of its berries, making it excellent for wine production. Heterozygous, it does not breed true from seeds, and by the Roman period early agriculturists had found that the best way to preserve grape plants with desired characteristics was through some form of woody propagation, producing distinct cultivars. Writing in the first century AD, Pliny the Elder described over 80 different varieties (Unwin 1996) and Lucius Columella observed that the same cultivar differed in production from vineyard to

vineyard, that some varieties were particularly suited to certain locations, and that some locations were better than others (Columella 1941). As Columella put it, a “vine...though only moderately fruitful should be our choice, if only we have a piece of ground where the flavor of the wine is distinguished and costly” (Columella 1941:235). The search for such locations in California, as well as the discovery of which varieties would produce the most flavorful wines in a given area, would become one of the driving forces behind vineyard expansion in California.

Although a desire for increased quality is one factor in vineyard expansion, the major impetus for vineyard development is economic. With a useful economic life of 30–40 years, and a three- to four-year pre-productive period, vineyards represent significant present investments balanced against expected future returns. The general pattern of vineyard establishment in California’s wine history has been that changes in supply or demand increase the price of wine, leading to an increased price for grapes as wineries attempt to outbid each other for a scarce resource. This period of scarcity generally lasts at a minimum for three to four years, since grape supply cannot be immediately increased. During this period of high prices, land owners and investors make individual decisions to plant vineyards. Generally in four to five years, the aggregate increase in plantings results in the production of more grapes than are required by the market. Grape prices fall and, in some cases, vineyards are abandoned and firms go out of business.

An examination of Figure 23.1, which presents California wine grape acreage in ten-year increments, shows at least four periods of expansion. The first, from 1870 to 1890, was the first major California wine boom and occurred primarily in the coastal areas of Northern California. *Vitis vinifera* cultivars were introduced and California winemakers sought to match variety with location. The second period, from 1920 to 1940, saw a doubling of acreage throughout California and was, paradoxically, the result of the United States National Prohibition Act in 1919. During this period variety selection in California was focused on those grapes with thick skins that could withstand shipping by railcar to the Midwest and East Coast states, or grapes with high levels of pigmentation, resulting in deeply colored wines that could be stretched by water additions. The third and fourth booms occurred between 1960 and 2000 and resulted from an increased consumption of table wine by American consumers. These booms saw the expansion of coastal and central valley vineyard acreage and the widespread planting of such varieties as Chardonnay, Cabernet Sauvignon, and Merlot. Bearing wine grape acreage grew from 291,000 acres in 1990 to 458,000 in 2000 (USDA NASS CFO 2008). During the period from 1970 to 1980, the demand was primarily for white grapes, such as Colombard, Chenin blanc, and Chardonnay. Conversely, in the decade of the 1990s, red grapes such as Cabernet Sauvignon, Merlot, and Syrah were demanded. Each boom period thus had its unique dynamics and resulted in expansion in some cultivars rather than in others.

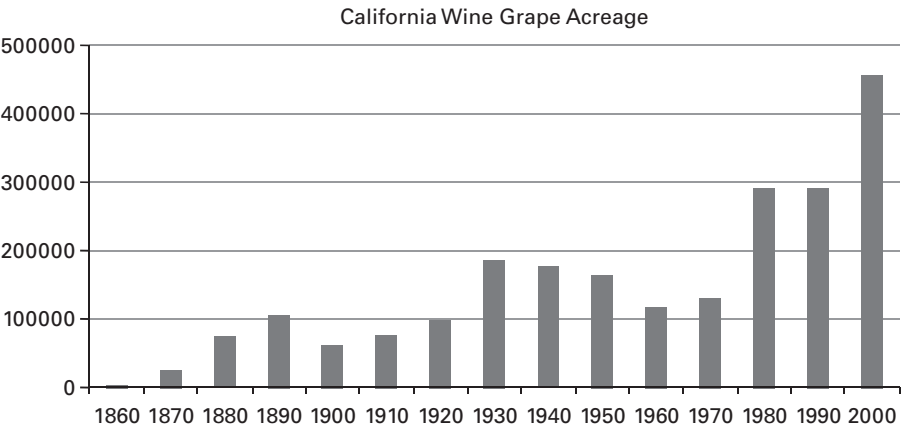


Figure 23.1. Acreage by decade of wine grape production in California from 1860 to 2000. Note on sources. The data for years 1920 to 2000 are of bearing acres and derived from the table “California Wine Grapes, 1920–2007” in *California Historic Commodity Data* (USDA NASS CFO 2008). The data for years 1860 to 1910 are derived from an unpublished study, which primarily used county boards of assessors’ figures and were for grapes of all types (Keefer 1995, unpublished). For this earlier period I have consistently omitted data from the Central Valley counties where from 1870 to 1910 grapes were primarily grown for table and raisin use. The data for 1860 to 1910 are thus internally consistent, but they perhaps slightly underestimate total wine grape acreage, as wine grapes were grown in the Central Valley in the nineteenth century.

Undoubtedly, the first *V. vinifera* variety introduced to California was the Mission variety, which was carried throughout the Americas by Franciscan and Jesuit friars, and is known as Criolla in Argentina (Amerine and Singleton 1977). For many years, most grape ampelographers assumed that Mission was not equivalent to any European variety, but rather had grown from seed in the Americas. This belief is reflected in the Argentine name for the grape, Criolla, as a Creole was a person of European ancestry who was born in the New World. Recently, DNA testing has shown that Mission is equivalent to the Spanish variety Listan Prieto (Tapia *et al.* 2007). Mission is a lightly colored red grape of relatively low acidity that produces a nondistinct wine. The Mission variety was most likely introduced to California at the Mission San Juan Capistrano, north of San Diego, in 1778 (Brady 1984). Since wine was required to celebrate the Eucharist, the Franciscan friars cultivated Mission grapes for wine production, taking the Mission variety with them as they moved northward establishing missions, ultimately ending in Sonoma. Following Mexican independence and the secularization of mission lands, the mission vineyards became the source of grape cuttings for European settlers in Alta California, who cultivated Mission for table grapes, home wine production, and brandy distillation. The first commercial wine production in California took place in Los Angeles in 1833 when Jean Louis Vignes, a native of the Bordeaux region in France, purchased property and began wine production (Pinney 1989). Vignes realized the shortcoming of Mission for

wine production and imported French varieties, although what types are unknown. Under Mexican rule, the small European population in California was primarily located in Southern California, as were the majority of the vineyards. The Mission variety had been spread throughout coastal California and later was to be referred to as “the native grape” to distinguish it from the “foreign” importations that were to come.

Following the discovery of gold in 1848, California’s population boomed, primarily in Northern California and its gateway city, San Francisco. California’s European-born population has been estimated to have been approximately 15,000 prior to the gold rush, but by 1850 it had grown to over 90,000, and by 1860 had reached 380,000 (De Bow 1853:972, Kennedy 1861:27). The dramatic increase in population led to a demand for food and supplies, and vineyards and wineries were established in the Sierra foothills and in the coastal counties surrounding San Francisco. The initial vineyards relied on the already available Mission, but early agriculturists quickly began importing European varieties. In Napa County in the early 1850s, Joseph Osborne acquired European varieties from the Eastern United States, including the variety that became known as Zinfandel.¹ By the mid 1850s, in the Carneros region south of Napa, the Thompson brothers had established a nursery, selling fruit trees and imported grape vines (Pinney 1989:265). By 1858 they were advertising 45 different varieties for sale. In Santa Clara County, south of San Francisco, Antoine Delmas established a vineyard and nursery in 1851, importing vines from Europe and the Eastern United States. Delmas is credited with introducing Cabernet Sauvignon and Merlot to California and by 1858 his nursery included over 100 distinct varieties, taking first prize for his collection at the 1859 California State Fair (Pinney 1989:265). That same year, a competitor, A.P. Smith, offered 100 “foreign” varieties for sale at his nursery in Sacramento (Pinney 1989:265).

Probably the most famous person to import *V. vinifera* grapes into California during this period was Agoston Haraszthy, the director of Buena Vista, a major winery in Sonoma County. Having advertised his intentions and solicited subscriptions, in 1861, Haraszthy traveled to Europe for the purpose of collecting and importing grapevines. The following year he listed 492 varieties for sale – a remarkable number, although undoubtedly some were the same varieties, but known by regional names (Pinney 1989:280). Clearly, by the early 1860s, an impressive diversity of European *V. vinifera* varieties was available to California vineyardists, should they have the funds and inclination to purchase and plant them. However, the most easily available, least expensive, and most widely planted variety continued to be the Mission. It was to remain so until the mid 1880s.

During the late 1870s and into the 1880s, the California wine industry experienced a boom that dramatically increased plantings, dethroning Mission as California’s major variety and moving Northern California into the viticultural forefront. The boom was a result of population growth in California, improved transportation with the completion of the transcontinental railroad in 1869, and, most importantly, increased demand for California wine from the East coast of

the United States as a result of *Phylloxera vitifoliae* (the root louse) in France. Phylloxera had appeared in France's Rhone Valley in the late 1860s and rapidly spread throughout France's major winegrowing regions. By the mid 1870s, French production had declined and exports were curtailed, opening the door for other producing regions (Unwin 1996). As demand and prices increased for wine, a planting boom occurred in California. The boom was primarily induced by increased profitability, but it was sustained by the prevalent notion that France's wine industry might be destroyed, and that California would become the major supplier of wine to the world as phylloxera moved across Europe, devastating its vineyards. The irony was that California, too, would experience phylloxera's devastation. The French varieties imported in the 1870s carried phylloxera with them, and in the mid-1880s northern California vineyards would succumb to the aphid.²

The extent of California's first wine boom is reflected in a variety of statistics. Most obvious was the increase in wine production. In 1870, California produced 1.8 million gallons of wine. Twenty years later, the volume had grown eight-fold, to 14.6 million gallons. Equally impressive was the rise of wine production in Northern California. In 1870, San Francisco Bay Area vineyards had produced just over 500,000 gallons of wine, roughly equivalent to that produced in Los Angeles County. By 1890 the Bay Area was producing 8.3 million gallons of wine to Los Angeles County's 1.3 million (data from the Report of the California State Board of Agriculture, 1911, Sacramento CA USA, 1912, as cited in Pinney 1989:313). A rising tide lifts all ships, and during the boom, vineyards were established throughout California, but the major increase occurred in two northern California counties: Napa and Sonoma. From just over 3,000 acres planted in 1870, Napa expanded to over 18,000 acres in 1890. The increase in Sonoma vineyard acreage was even greater, growing from just over 5,000 acres in 1870 to just under 23,000 acres in 1890 (Keefer 1995, unpublished manuscript).

As impressive as the expansion in acreage was the increase in the diversity of grapes being grown. Varieties originally imported in the 1850s and 1860s were adopted and planted during the boom. Eugene Hilgard, Professor of Agriculture at the University of California, listed some of the commercial wine varieties he and his staff had analyzed in the years 1887–9. The list was long and the red wines examined included Malbec, Cabernet Franc, Cabernet Sauvignon, Tannat, Merlot, Gamay, Black Pinot [Pinot noir], Pinot Meunier, Chaucier Noir, Barbera, Freisa, Bonarda, Nebbiolo, Refosco, Araman, Cinsault, Grenache, Mondeuse, Moursatel, Mataro, Trosseau, Sirah, Ploussard, Carignane, Grossblau, and Zinfandel (Hilgard 1890:256). By 1888, Napa's acreage had grown to just under 16,000 acres. The dominant variety, at 5,700 acres, or one-third of all plantings, was Zinfandel. Fallen to second place, with 2,000 acres, was Mission. "Miscellaneous Reds" accounted for 1,600 acres and "Bordeaux Reds" had been set out on 779 acres. "Bordeaux Whites", which should have included Semillon, Sauvignon blanc, and Sauvignon Vert, took 400 acres. Over 2,600 acres were planted to "Riesling" of some type; another 2,600 were planted in "Miscellaneous Whites",

which would have included Burger and Palomino (which was known as Golden Chasselas) (Board of State Viticultural Commissioners 1888:44). The variety diversity was truly impressive and represented a definite movement toward improved quality, although growers were still uncertain as to where varieties should be planted: in Napa County, cool-weather varieties such as Riesling were often planted adjacent to warmer-weather varieties such as Cabernet Sauvignon. Had the boom continued, no doubt California growers would have learned where to plant which varieties for best varietal expression, but in the late 1880s, prices began to fall.

By the mid 1880s, the fruit from California's planting frenzy of the late 1870s and early 1880s came to market. The East Coast wine market might have been able to accept California's increased production, except that French wine was now becoming available, as French producers had begun replanting their vineyard on resistant rootstock. Coincidental with the decline in prices was the discovery that California, like France, was suffering from phylloxera. If vineyards were to survive, they would need to be replanted on resistant rootstock. The final nail in the coffin for California producers was the 1893 depression in the USA, which reduced credit availability and curtailed demand. California vineyard owners who had borrowed to plant vineyards in the early 1880s now faced the reality of low prices and dying vines. Many owners simply walked away from their debts, and California's first wine boom had ended.

California's second major boom occurred, paradoxically, during Prohibition. During the late nineteenth and early twentieth century, the United States had experienced a series of socially dislocating forces including major immigration, urbanization, and industrialization. Prohibition, the abolition of commercial production and sale of alcoholic beverage, had been advocated as a general solution to social problems and in 1919 the Eighteenth Amendment to the United States Constitution was ratified, becoming effective on 16 January 1920. California wine grape growers assumed that they had lost their market, as commercial wineries were forced out of business. However, the enabling legislation to enforce the Amendment, the Volstead Act, allowed the home production of "non-intoxicating" fruit juices made from apples and grapes. Under this exemption, home winemaking flourished, creating an increased demand for California grapes (Lapsley 1996). As in most booms, grape prices increased, leading to new plantings throughout California.

The major producers of home-made wine were immigrants from Southern Europe who had streamed into the United States during the 1890s and 1900s, settling in Eastern and Midwest cities. For them, wine was a necessary staple, like bread or cheese. In 1918, the last year of commercial production, wine grapes had sold for US\$30 a ton. In 1919 and 1920, California vineyard owners were approached by grape brokers who proposed to buy their crop for between US \$70 and US\$90 a ton and ship it to Eastern cities on rail cars, where they would in turn sell the grapes to immigrant winemakers. High grape prices led to increased planting. In 1920, California had 98,500 bearing acres of wine grapes. A decade

later, it had almost doubled to 188,000 acres (USDA NASS CFO 2008). However, although acreage had expanded, the selection of grape varieties had changed and narrowed when compared to the diversity of varieties during the 1880s.

Varietal choice in the 1920s was a response to consumer demand and the realities of rail transportation. Immigrant home-winemakers were interested in making a table beverage as cheaply as possible, not in producing high-quality wine. They would often “stretch” their grapes by taking the pressed skins and seeds after the first fermentation, adding water and sugar, and refermenting the mixture, producing a second wine that could then be blended with the first production. Under such circumstances, a ton of grapes could produce 300 gallons of “wine”, rather than the 150–160 gallons normally produced from a ton. The type of grapes desired were either those that were inexpensive, or which contained higher than normal amounts of tannin and pigmentation, allowing for dilution with water. Additionally, the grapes had to have sufficiently thick skins to be able to be loaded into 50-pound lug boxes and shipped east in boxcars. Thin-skinned varieties such as Cabernet or Riesling fell from favor and were grafted to Petite Sirah, which possessed sufficient tannin that it could be diluted, or to *teinturier* varieties, such as Alicante Bouschet and Grand Noir, which contain pigmentation in the juice, as well as in the skins. Carignane, an inexpensive red variety that could bear heavy crops when pruned long, gained in popularity, as did the ever-present Zinfandel. By repeal of Prohibition in 1933, as a result of new plantings and grafting, the composition of California’s vineyards had changed dramatically from that of the 1880s. For example, in Napa County 40% of the acreage was planted to Petite Sirah, followed by Alicante Bouschet at 25%. Together these two varieties composed over two-thirds of Napa’s acreage, with the balance being composed of Zinfandel and Carignane (Marquis 1934:10, as quoted in Lapsley 1996:43).

As with most boom cycles, California vineyardists ultimately planted more acres of grapes than demanded by the market. The high grape prices of the early 1920s encouraged plantings throughout California. By 1926 and 1927, grape prices dropped to US\$45 a ton, down from the highs at the beginning of the decade, and planting slowed, but plantings from 1923, 1924, and 1925 were not yet bearing fruit and so production continued to increase. By 1930 prices fell to US\$20 a ton and California’s bearing wine grape acreage peaked at 188,000 acres. Repeal of Prohibition, although making wine production legal once more, did not increase wine consumption, although it did reduce home production. Commercial wine production was renewed at the depth of the Depression, a terrible time to begin any business, and the legacy of Prohibition was tens of thousands of acres of poorer-quality varieties spread across California. Throughout the 1930s wine consumption languished, grape prices remained depressed, and vineyard acreage declined. It would take almost 30 years for the recovery to begin.³

Although the 1930s were a grim period for California wine producers, it was an important time for research. Throughout the 1930s and into the 1940s, Drs. Albert Winkler and Maynard Amerine of the University of California’s Department of Viticulture conducted a series of experiments that would ultimately dramatically

improve varietal wine production in California. The professors ranged throughout the state, identifying grape varieties and then producing small lots of varietal wines from different geographic areas. These wines were then analyzed for acidity, color, and alcohol, and evaluated for varietal intensity and overall quality. Winkler and Amerine also collected temperature data for various California locations, creating a “degree-day” model that allowed California regions to be compared for levels of heat during the grape’s growing season. Combining the result of sensory and chemical analysis of the wines with temperature data, the professors were able to quantify and to describe the effects of temperature on grape composition by variety. Based on their research, Winkler and Amerine divided California into five climatic grape-growing regions and then made specific suggestions as to which varieties should be planted in which regions. Their research remains a landmark in the history of California viticulture, recommending specific grape varieties and suggesting a way of thinking about wine quality that provided a basis for the wine revolution of the 1960s (Amerine and Winkler 1944).

From the 1960s on, California experienced two wine booms (Figure 23.1 and USDA NASS CFO 2008). From 1960 to 1980, wine grape acreage more than doubled from 118,000 acres in 1960 to over 290,000 acres in 1980. The 1980s saw essentially no growth, but from 1990 to 2000, grape acreage increased by 167,000 acres to 458,000 acres. Wine had become so popular that by 1972, Time Magazine put the Gallo brothers on their November 27 cover and ran a lead story entitled “American Wine: There’s Gold in Them Thar Grapes”. It is much easier to document the extent of the wine boom in the United States than it is to explain why it occurred. The period of the late 1960s and early 1970s was both a time of affluence and cultural upheaval for America, as the Baby Boom generation came of age and America experienced the socially dislocating effects of the Vietnam War. Simply put, for a variety of reasons some Americans began consuming table wine as their main form of alcohol and American interest in wine is perhaps best considered as one part of a massive cultural shift that took place in the late 1960s and early 1970s (Lapsley 1996:196–201).

The boom in wine consumption during the late 1960s and early 1970s was primarily in white table wine, which had benefited from improved technology in the 1950s and early 1960s. Prior to the 1960s, the dominant form of wine consumed in the United States was fortified wine, that is, wine such as “port” or “sherry” that derived most of its flavor from oxidation and alcohol, accounting for over 70% of all wine consumed (Lapsley 1996:137). During the 1950s, new technology was introduced into the California industry, including stainless steel fermentors, pure yeast cultures, cold fermentations, and sterile bottling. The result of these innovations was the production of fruity white wines with a touch of residual sweetness, wines that bore no resemblance to fortified wines. For a generation that had been raised on soft drinks and had now come of legal drinking age, these fruity and slightly sweet white wines were a natural progression. Between 1970 and 1980, per capita consumption of all wine grew by 1.2 gallons to 2.38 gallons. White wine accounted for more than

80% of that growth, increasing from 0.27 gallons to 1.26 gallons (M. Shanken Communications 2005:203).

In order to maximize the possibilities inherent in the new white wine production techniques, California winemakers turned away from varieties that had been used for dessert wine production and instead sought productive white varieties with fruity aromas. In the 1970s, the majority of the new white wines were produced from Colombard and Chenin Blanc planted in the 1960s in California's warm Central Valley. By 1980, these two varieties composed one-quarter of all California acreage with Colombard dominating because of its ability to maintain acidity when grown in hot climates. In the cooler coastal areas, such as Napa and Sonoma Counties, and in the newly planted regions of Monterey and Santa Barbara Counties, Chardonnay became the dominant white variety. Unlike Colombard and Chenin Blanc, which were usually marketed as "California Chablis", Chardonnay was generally retailed under its own varietal name and grew in popularity. For many wine consumers, varietal labeling became a signal of quality, and Chardonnay rapidly became the best-known white varietal. By 1990, Chardonnay was being widely planted in the Central Valley and had passed Colombard as the most planted white grape. In 2005, Chardonnay remained the undisputed king of all white grapes, accounting for 70% of all varietally labeled white wine sales in the United States (M. Shanken Communications 2005:208).

The boom of the 1990s differed from that of the 1970s in that the demand was for red wine. But, like the earlier white wine boom, it was driven by the major United States' demographic group: the Baby Boomers. By the 1990s, this demographic group was entering middle age and becoming concerned about health in general and especially cardiovascular disease. In 1991 the USA television news program 60 Minutes, a program of CBS News, reported on a phenomenon referred to as "the French Paradox". The paradox was that the French consumed as much fat as Americans, but experienced a much lower rate of strokes and heart attacks. Some physicians speculated that the reason for the lower rate of cardiovascular disease among the French was that the French consumed red wine at higher rates than did Americans. For aging American Baby Boomers who were concerned about cardiovascular health, the 60 Minutes program gave them license to drink red wine, allowing them to perceive wine consumption as beneficial to their health. During the decade of the 1990s, per capita consumption of red wine almost tripled, rising from 0.35 gallons in 1990 to 1 gallon in 2000 and accounting for all of the per capita growth in wine consumption during the decade (M. Shanken Communications 2005:203).

As in other booms, the demand for red wine increased prices and encouraged plantings throughout California. Total acreage of wine grapes grew by just over 50%, as California grape growers set out over 150,000 acres of new plantings, bringing the 2000 total acreage to 458,000 acres (CASS 1992, 2001). Although various red varieties were planted, Cabernet Sauvignon and Merlot were the two varieties most favored. Cabernet Sauvignon acreage doubled, from just over 34,000 acres in 1990 to just under 70,000 acres in the year 2000. Merlot, a red

Bordeaux variety which had been considered a specialty wine, grew six times in acreage, expanding from 8,188 acres in 1990 to 49,986 acres in 2000. Together, Cabernet Sauvignon and Merlot accounted for approximately half of the vineyard expansion of the 1990s. Both varieties had originally been planted in California's cooler coastal counties and in 1980, these coastal counties had counted for more than 80% of all Cabernet and Merlot acreage. However, by 2000, these varieties were planted throughout California, with California's warm interior valley claiming well over one-third of the acreage and perhaps half of the actual grape production (CASS 1992, 2001). In 2008, these two red varieties accounted for more than 70% of all varietally labeled red wine consumed in the United States (M. Shanken Communications 2005:208).

Today, in 2008, the search for, in Columella's words, "a piece of ground where the flavor of the wine is distinguished and costly" has been largely accomplished in California. Price differences are so great between the same variety grown in different grape pricing districts that in some ways a grower in one district is in a completely different business than a grower in another district. Take, for instance, the example of Cabernet Sauvignon. In 2007, the average price paid for a ton of Cabernet Sauvignon in the district that consists only of Napa County was US \$4,144. In the neighboring district to the west (the combined Counties of Sonoma and Marin), the price was US\$2,204. Thirty miles to the southeast of Napa County, in the district that consists of southern Sacramento and northern San Joaquin Counties, the price was US\$339 a ton. And at the southern end of California's Central Valley, in the district that consists of the combined area of southern Kern and Tulare Counties and the entire King County, Cabernet Sauvignon sold for only US\$126 a ton (CDFA 2008a,b). The price difference between grapes grown in the cooler coastal county districts and those grown in the warm, interior valley districts is such that wine grape production in the two regions is best viewed as two distinct businesses. The truth of this view is made obvious when volume produced is compared with dollars received. The coastal districts produced 24% of all grapes harvested for wine in 2007, but received 66.8% of all dollars. The interior districts, because of much higher production per acre, delivered 76% of all grapes crushed for wine, but because of the low prices paid for its grapes, received only 33.4% of all revenue (CDFA 2008a,b).⁴

From a perspective of colonizing land, *V. vinifera* has been extremely successful in California, in a little over two centuries covering today over 500,000 acres (or about 848,000 acres if raisin and table grapes are included) (CASS 2008). For some of the growers who have partnered with *V. vinifera*, grape growing has been and remains a very successful business. For others, who have planted at the wrong time in a cycle, or chosen what turned out to be an unpopular variety, or purchased a piece of ground where the flavor of the wine was not distinguished or costly, the investment in vineyards has not provided expected returns. Ultimately vineyards are businesses, concrete expressions of an individual's belief in the future. The history of California's wine industry reminds us that consumer demand can change, that varieties and types of wine can and do go in and out

of fashion, that government policies, such as Prohibition, can dramatically affect profitability,⁵ and that increased or decreased production outside the United States can alter internal demand for domestic wine, something of particular importance in an increasingly global economy.

Despite these caveats, the future of the plant–human partnership seems strong. The per capita consumption of wine in the United States continues to grow and is still only half that of countries such as the United Kingdom or Australia, and quite far below that of traditional wine-drinking countries such as France or Italy. The children of the Baby Boomers, the so-called “Millennials” are the next major demographic wave in the United States, and they are increasingly choosing wine.⁶ Although wine grape growing and winemaking is expanding beyond California, it is California of all the states that has the necessary moderate climate that reduces grower risks while producing ripe and flavorful grapes. Given the expected increases in both population and per capita consumption of wine, the future of the human–plant partnership that is grape growing seems secure in California.

Notes

- 1 I do not mean to imply that Osborne was the first to bring Zinfandel into California. The introduction of Zinfandel to California is fully discussed by Sullivan (2003).
- 2 There is some disagreement among researchers as to whether phylloxera was already present in California, or was imported with European varieties, either from Europe or nurseries in the Eastern USA.
- 3 For the sake of historical accuracy, it should be noted that there was a brief increase in wine prices and plantings during World War II; however, it is beyond the scope of this chapter to discuss the period.
- 4 Calculations were made by author by taking average price per ton for each crush district (Table 7, “Weighted Average Grower Returns” of the 2007 California Grape Crush Report) and multiplying by average tons per region, (Table 2, “Tons of Grapes Crushed by California Processors” of the 2007 California Grape Crush Report. For this comparison, districts 1, 2, 3, 4, 5, 6, 7, 8, and 16 were considered coastal and districts 9, 10, 11, 12, 13, 14, 15, and 17 were considered interior. See CDFA, 2008b.
- 5 One of the reasons for the decline in per-capita consumption of wine in the 1980s was an anti-alcohol policy on the part of the US Federal Government, as seen in such actions as a decrease in the legal level of blood alcohol when driving, a grouping of alcohol with illegal drugs (“Just Say No!”), and the imposition of warning labels on alcoholic beverages.
- 6 A wine industry group, The Wine Market Council, has been tracking consumer attitudes towards wine for the past 16 years. For information on Millennials and wine see <http://winemarketcouncil.com/research.asp>.

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24 Genetic Resources of Yeast and Other Micro-Organisms

C.W. Bamforth

Micro-organisms have been employed in the production of foodstuffs for millennia, but only knowingly so since the work of scientists such as Charles Cagniard-Latour, Theodor Schwann, Friedrich Kützing, and Louis Pasteur (Anderson 1995, Barnett 2003). As recently as 1839, the likes of Liebig and Wohler were ridiculing the concept that alcoholic fermentation was anything other than a basic piece of chemistry (Anonymous 1839). And yet for the longest time, processes such as beer fermentation employed “back slopping” in which a proportion of a successful brew was added back to a new brew to “kick-start” it. They were unwittingly priming with the yeast that had multiplied in the previous batch – and they pronounced that this *barm* from the foamy heads of the vessel signified *godesgoode* “because it cometh of the grete grace of God” (David 2001).

Legras *et al.* (2007) argue for diversity in *Saccharomyces* founded upon human history. They draw attention to genetic relatedness between strains, with bread yeasts displaying a genetic make-up intermediate between beer and wine strains, with the strains used for the production of rice wine and sake being closely related to beer and bread strains. However they emphasize that local domestication makes a sizeable contribution to the genetic diversity. In the case of wine yeasts, for instance, they propose that the organism followed the migration of humans and their vines.

It was Emil Christian Hansen (1842–1909), working in the Carlsberg Laboratories, who pioneered pure cell technology and whose strategies forged the way for all ensuing fermentation-based industries, from beer to modern biotechnological delivery of diverse products. Even Hansen’s concepts were not universally embraced, the English insisting that they needed more than a single strain to produce their beers: one yeast for primary fermentation and the other to bring the beer into condition (carbonation). The second yeast was named for the British (*Brettanomyces*), and there are still a handful of brewers today who embrace its use, including one California-based outfit which boasts “...if used properly with care, it can add rich aromas and flavors of earthiness, leather, smoke, barnyard, & our favorite descriptor – wet dog in a phone booth” (Russian River 2008).

Fermentation processes are employed in the production of various entities: foods and beverages (Bamforth 2005; Table 24.1); health-care products; enzymes and industrial chemicals; and fuels (Waites *et al.* 2001). Arguably, the most extensively researched of these processes is the production of beer.

1 Yeasts

Saccharomyces strains, capable of producing ethanol and carbon dioxide as end products of carbohydrate metabolism when growing fermentatively, have been isolated from a great many sources (Table 24.2). There are primarily two strains of this organism that are employed for the brewing of beer: *Saccharomyces cerevisiae*, the so-called top-fermenting yeast, for ales, and *Saccharomyces pastorianus* for lagers, a yeast that historically is cropped from the bottom as opposed to the top of fermenters (Table 24.3; Boulton and Quain 2001). Whereas ale strains through the millennia have been isolated in a great many locales, the much more limited number of lager strains were isolated in Bavaria and found their way through the world of brewing by diverse routes that in the first instance were tantamount to smuggling! The genome of *S. pastorianus* is somewhat the more complex and it is believed that this organism arose from a melding of *S. cerevisiae* and *S. bayanus* (Vaughan Martini and Martini 1993).

Many brewers are fastidious about their use of yeast strain, fashioning their process around the characteristics of their own particular line in respect of flavor delivery, flocculation characteristics, and so on. The reality is that it is only for beers that do not have robust malt and hop characters that the more subtle flavor-active substances elaborated by the yeast can be detected. There are, however, certain yeast strains that produce relatively unique characteristics. For example, the ale strains that are used to make wheat-beers in Bavaria are the only brewing yeasts that elaborate ferulic acid decarboxylase, an enzyme that converts the ferulate from grain into 4-vinylguaiacol, the latter possessed of a distinctive clove-like character (McMurrough *et al.* 1996). There are also some beers that depend on diverse micro-organisms for their production. Notable amongst them are the lambic and gueuze products of Belgium, in which instance the microflora comprises some or all of Enterobacteria, *Kloeckera apiculata*, *S. bayanus*, *S. globosus*, *S. dairenensis*, *Pedococcus damnosus*, *P. cerevisiae*, *Lactobacillus*, *Brettanomyces lambicus*, *B. bruxellensis*, *Candida*, *Hansenula*, and *Pichia*, as well as *S. cerevisiae* and *S. pastorianus* (Verachtert 2002).

With regard to mainstream brewing strains, then, there are diverse sources world-wide (Table 24.4). Most companies will maintain their own “house strains” and perhaps use them 5–10 times at most for successive fermentations – i.e., re-pitching a new batch of wort with yeast grown in the previous fermentation. This is possible because of the relatively low alcohol contents developed in most brewery fermentations: at higher alcohol concentrations (c.f. those in the wine industry) the yeast is too unhealthy at the end of fermentation for re-use. When it

Table 24.1. Some examples of organisms used in foodstuff production

Organism	Type of organism	Foodstuff	Further reading ^a
<i>Acetobacter aceti</i>	Bacterium	Vinegar	Raspor and Goranovic 2008
<i>Aspergillus oryzae</i>	Mould	Miso, soy sauce, sake	Inoue <i>et al.</i> 1992
<i>Brevibacterium linens</i>	Bacterium	Cheese pigment and surface growth	Law 1997
<i>Lactobacillus casei</i>	Bacterium	Cheese and other fermented dairy products	Robinson 1986
<i>L. curvatus</i>	Bacterium	Sausage	Campbell-Platt and Cook 1994
<i>L. delbrueckii</i> ssp. <i>bulgaricus</i>	Bacterium	Cheese, yoghurt	
<i>L. helveticus</i>	Bacterium	Cheese and other fermented dairy products	
<i>L. lactis</i>	Bacterium	Cheese and other fermented dairy products	
<i>L. plantarum</i>	Bacterium	Fermented vegetables, sausage	
<i>L. sakei</i>	Bacterium	Sausage	
<i>L. sanfranciscensis</i>	Bacterium	Sourdough bread	
<i>Leuconostoc lactis</i>	Bacterium	Cheese and other fermented dairy products	
<i>L. mesenteroides</i>	Bacterium	Fermented vegetables, cheese and other fermented dairy products	
<i>Oenococcus oeni</i>	Bacterium	Wine	
<i>Pediococcus acidilactici</i>	Bacterium	Fermented vegetables, sausage	
<i>P. halophilus</i>	Bacterium	Soy sauce	Steinkraus 1996
<i>P. pentosaceus</i>	Bacterium	Sausage	
<i>Penicillium camemberti</i>	Mould	Surface ripening of cheese	
<i>P. chrysogenum</i>	Mould	Sausage	
<i>P. roqueforti</i>	Mould	Blue-veined cheeses	
<i>Propionibacterium freudenreichii</i>	Bacterium	Eyes in Swiss cheese	
<i>Rhizopus microsporus</i>	Mould	Tempeh	
<i>Saccharomyces cerevisiae</i>	Fungus	Bread, ale, wine, cider	Hanneman 1980, Briggs <i>et al.</i> 2004, Fleet 1993, Lea and Drilleu 2003
<i>S. pastorianus</i>	Fungus	Lager	Boulton and Quain 2001
<i>S. sake</i>	Fungus	Sake	Inoue <i>et al.</i> 1992

Table 24.1. (cont.)

Organism	Type of organism	Foodstuff	Further reading ^a
<i>Staphylococcus carnosus</i>	Fungus	Meat	
<i>Streptococcus thermophilus</i>	Bacterium	Cheese, yoghurt	
<i>Tetragenococcus halophila</i>	Bacterium	Soy sauce	
<i>Zygosaccharomyces rouxii</i>	Bacterium	Soy sauce	

Note:

^a References cited only once: e.g., for all organisms relevant to cheese, see Law 1997.

Table 24.2. Sources of *Saccharomyces*

<i>Saccharomyces</i>	Source
<i>S. barnettii</i>	Sauerkraut, soft drink
<i>S. bayanus</i>	Fruit juice, beer, perry, grape must
<i>S. cariocanus</i>	<i>Drosophila</i> spp.
<i>S. castellii</i>	Soil, baboon caecum, buttermilk
<i>S. cerevisiae</i>	Wine, beer, fruit, soil, soft drinks, man
<i>S. dairenensis</i>	Fermenting grapes, dry fruit
<i>S. exiguus</i>	Grape must, sewage, soil
<i>S. kluyveri</i>	Soil, <i>Drosophila</i> spp., tree exudate
<i>S. kudriavzevii</i>	Decayed leaf
<i>S. kunashirensis</i>	Soil near hot spring
<i>S. martiniae</i>	Fermenting mushroom
<i>S. mikatae</i>	Decayed leaf, soil
<i>S. paradoxus</i>	Oak tree exudates, soil
<i>S. pastorianus</i>	Beer
<i>S. rosinii</i>	Soil
<i>S. servazzii</i>	Soil, man with HIV
<i>S. spencerorum</i>	Soil, larval gut
<i>S. transvaalensis</i>	Soil
<i>S. unisporus</i>	Kefyr, cheese

Source: Walker 1998.

is necessary to pitch “new” yeast into a fermentation it is grown up from a master vial (usually preserved in liquid nitrogen) through successive cultures of increasing volume (Stewart 2006).

Brewers are temperamentally resistant to the use of gene technology in the development of new strain opportunities. The adherence to “clean labeling” principles is manifest. Nonetheless there has been ample work on genetic modification of brewing strains (itself a challenge because of the polyploidy or aneuploidy of these organisms) (Hammond 1998).

Table 24.3. Differentiation of ale and lager yeast brewing strains

	Ale yeast	Lager yeast
Species	<i>S. cerevisiae</i>	<i>S. pastorianus</i>
Genome size	1	1.5
Maximum growth temperature (°C)	≥37	≤34
Melibiose hydrolysis	no	yes
Fructose transport	facilitated	active
Maltotriose utilization	generally poor	generally good
Growth between 6 and 12°C	poor	good

Source: after Quain 2006.

Table 24.4. Commercial sources of brewing yeast

Collection	Web address
Belgian Co-ordinated Collections of Micro-organisms (BCCM)	http://bccm.belspo.be/index.php
National Collection of Yeast Cultures	http://www.ncyc.co.uk
Research Institute of Brewing and Malting (RIBM)	http://www.beerresearch.cz/encollyeats.htm
Siebel Pure Yeast Library	http://www.siebelinstitute.com/services/yeast.html
VTT	http://culturecollection.vtt.fi/nomenclature.html
White Labs	http://www.whitelabs.com/
Wyeast	http://www.wyeastlab.com/

There is an increasing interest in the use of dried yeast delivery to breweries directly from yeast companies (Muller *et al.* 1997). Dried yeast has been much more extensively used in wine production, an industry that frequently appears to be far less fastidious about its yeast than is the case in brewing, insofar as far more attention seems to be paid to the grape stock. Indeed, the surface of the grape *Vitis vinifera* harbors a wide range of micro-organisms, including *Saccharomyces*, and historically advantage has been taken of this endogenous microflora for the production of wine (Pretorius 2000). However the reality is that *S. cerevisiae* is by no means the predominant yeast on the grape and it has been suggested that the main “natural” source of the yeast owes to the colonization of the vessels and buildings used to ferment grape juice. The principal strains used as added cultures for wine-making are *Saccharomyces cerevisiae*, *S. bayanus*, *Zygosaccharomyces bailii*, *Schizosaccharomyces pombe*, and *Torulaspora delbrueckii* (flor yeast) (Jackson 2008). Consideration of the work of Pretorius (2000) highlights the similarities in approaches taken to the study of beer and wine yeasts.

Table 24.5. Micro-organisms and cheese production

Cheese type	Organisms
Italian grana and pasta types, Swiss	<i>Thermophilics</i> <i>Lactobacillus delbrueckii</i> ssp. <i>bulgaricus</i> <i>Lactobacillus helveticus</i> <i>Streptococcus thermophilus</i>
Blue, Cheddar, cottage, cream, Gouda, Limburger	<i>Homofermentative</i> <i>Lactococcus lactis</i> ssp. <i>cremoris</i> <i>Lactococcus lactis</i> ssp. <i>lactis</i> <i>Lactococcus lactis</i> ssp. <i>lactis</i> biovar <i>diacetylactis</i>
Blue, cottage, cream, Gouda	<i>Heterofermentative</i> <i>Leuconostoc mesenteroides</i> ssp. <i>cremoris</i>

Source: Fox 1993.

2 **Lactic acid bacteria**

The lactic acid bacteria (LAB) comprise acid-tolerant Gram-positive bacteria found in decomposing plants and dairy products that produce lactic acid as the major end-product of carbohydrate metabolism (Salminen *et al.* 2004). This acidification has been taken advantage of through the millennia to preserve foods through the inhibition of undesirable organisms, including pathogens. In turn the organisms contribute beneficial characteristics to those foodstuffs.

Lactic acid bacteria can be divided into the homofermentative bacteria that produce a single end-product, lactic acid, from fermentation of carbohydrates, and the heterofermentative bacteria that produce more than lactic acid alone, including carbon dioxide and ethanol.

The lactic acid bacteria have been exploited as prebiotics (Tannock 2005); in dairy, meat, fish, and vegetable fermentations; in the production of soy sauce; for the malolactic fermentation in wine production (Boulton *et al.* 1999); and for the commercial production of the antibiotic nisin (Jack *et al.* 1994) and thickener polysaccharides (Baird and Pettit 1991). They are important alongside other organisms for the production of cheeses (Fox *et al.* 2000; Table 24.5) and sour-dough bread (Pylar 1988; Table 24.6).

3 **Microbial biomass protein**

Although long heralded as an opportunity for the conversion of abundant, low-cost carbon sources into protein for animal and human feed (Goldberg 1985; Table 24.7), the commercial realization of microbial biomass protein has been very limited – although it is a reality as co-products in other industries – e.g., surplus yeast from brewery fermentations (Huige 2006).

Table 24.6. The microflora of sourdough production***Homofermentative organisms****Lactobacillus acidophilus**L. casei**L. farciminis**L. plantarum****Heterofermentative organisms****L. brevis**L. brevis* var. *lindneri**L. buchneri**L. fermentum**L. fructivorans****Yeasts****Candida crusei**Pichia saitoi**Saccharomyces cerevisiae**Torulopsis holmii**Source:* Röcken and Voysey 1995.**Table 24.7.** Microbial biomass protein opportunities

Substrate	Organism
Cellulose	<i>Alcaligenes</i> , <i>Cellulomonas</i>
Ethanol	<i>Candida utilis</i> , <i>Acinetobacter calcoaceticus</i>
Glucose	<i>Fusarium venenatum</i>
Hydrocarbons	<i>Candida tropicalis</i> , <i>Yarrowia lipolytica</i>
Methane	<i>Methylococcus capsulatus</i>
Methanol	<i>Methylomonas clara</i> , <i>Methylophilus methylotrophus</i> , <i>Pichia pastoris</i>
Molasses	<i>Candida utilis</i>
Starch	<i>Saccharomyces cerevisiae</i> , <i>Saccharomycopsis fibuligera</i> / <i>Candida utilis</i>
Sucrose	<i>Candida utilis</i>
Sulphite waste liquor	<i>Candida utilis</i>
Whey	<i>Candida intermedia</i> , <i>C. krusei</i> , <i>C. pintolepesii</i> , <i>C. utilis</i> , <i>Kluyveromyces lactis</i> , <i>K. marxianus</i> , <i>Lactobacillus bulgaricus</i>

Sources: Batt and Sinskey 1984, Trinci 1991.

The success of any commercial operation seeking to convert into protein either a waste stream, such as whey from the cheese industry (Gonzalez Siso 1996), or a mainstream chemical industry feedstock, such as methanol (Schrader *et al.* 2009) is intimately dependent on prevailing economic considerations.

Table 24.8. Other uses for micro-organisms

	Bacteria	Yeasts and filamentous fungi
Gibberellins		<i>Fusarium moniliforme</i>
Fungicides		<i>Coniothyrium minitans</i>
Insecticides	<i>Bacillus thuringiensis</i>	
Silage	Lactic acid bacteria	
L-glutamine	<i>Corynebacterium glutamicum</i>	
L-lysine	<i>Brevibacterium lactofermentum</i>	
L-tryptophan	<i>Klebsiella aerogenes</i>	
α -Amylase	<i>Bacillus subtilis</i>	
β -Amylase		<i>Aspergillus niger</i>
Glucoamylase		<i>Aspergillus niger</i>
Glucose isomerase	<i>Streptomyces olivaceus</i>	
Invertase		<i>Kluyveromyces</i> spp.
Lactase		<i>Kluyveromyces lactis</i>
Cellulases		<i>Trichoderma viride</i>
Lipases		<i>Candida cylindraceae</i>
Pectinases		<i>Aspergillus wentii</i>
Subtilisin	<i>Bacillus licheniformis</i>	
Neutral proteinase		<i>Aspergillus oryzae</i>
Microbial rennet		<i>Rhizomucor miehei</i>
Acetone	<i>Clostridium</i> spp.	
Butanol	<i>Clostridium acetobutylicum</i>	
Ethanol	<i>Zymomonas mobilis</i>	<i>Saccharomyces cerevisiae</i>
Glycerol		<i>Zygosaccharomyces rouxii</i>
Methane	Methanogenic archaeans	
Alginates	<i>Azotobacter vinelandii</i>	
Cellulose	<i>Acetobacter xylinum</i>	
Dextran	<i>Leuconostoc mesenteroides</i>	
Gellan	<i>Sphingomonas paucimobilis</i>	
Polyhydroxybutyrate	<i>Ralstonia eutropha</i>	
Pullulan		<i>Aureobasidium pullulans</i>
Scleroglucan		<i>Sclerotium rolfsii</i>
Xanthan	<i>Xanthomonas campestris</i>	
Human growth hormone	Recombinant <i>Escherichia coli</i>	Recombinant <i>Saccharomyces cerevisiae</i>
Insulin	Recombinant <i>Escherichia coli</i>	Recombinant <i>Saccharomyces cerevisiae</i>

Source: Ratledge and Kristiansen 2006.

4

Other uses for micro-organisms

There are diverse other industrial fermentation processes (Table 24.8; Yu 1990). To these may be added the production of nucleotides, organic acids, vitamins, alkaloids, antibiotics, steroids, vaccines, and immunosuppressants.

Table 24.9. Some culture collections

Collection	Organisms	Web address
American Type Culture Collection (ATCC)	All types	http://www.atcc.org
CABI Bioscience	Filamentous fungi	http://www.cabi-bioscience.org
Centraalbureau voor Schimmelcultures	Filamentous fungi and yeasts	http://www.cbs.knaw.nl/
Collection Nationale de Cultures de Microorganismes	All types	http://www.pasteur.fr/recherche/unites/Cncm/index-en.html
Die Deutsche Sammlung von Mikroorganismen und Zellkulturen	All types	http://www.dsmz.de/
Herman J. Phaff Culture Collection	Yeasts and fungi	http://www.phaffcollection.org/
Enology Culture Collection	Wine yeasts	http://wineserver.ucdavis.edu/content.php?category=Research&id=367
National Collection of Industrial and Marine Bacteria	Bacteria	http://www.ncimb.co.uk
National Collection of Yeast Cultures	Yeasts	http://www.ncyc.co.uk

5

Collections of micro-organisms

A series of culture collections is available for the sourcing of this rich diversity of micro-organisms (Table 24.9).

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25 Biodiversity of Native Bees and Crop Pollination with Emphasis on California

Robbin W. Thorp

The often-cited estimate that about 30% of our diet depends directly or indirectly on crops pollinated by animals (McGregor 1976) may not hold with more recent and future analyses (Klein *et al.* 2007). But much of the variety in our diet beyond staples such as wind-pollinated grains depends on animals, especially bees, for pollination. Such pollinator-dependent crops include many fruits (pome, stone), berries (cane, bramble), cucurbits (melons, squashes), nuts (almond, macadamia) and vegetable, oil, and forage crop seeds.

Analyses of primary data from 200 countries found that over 75% of 87 globally important food crops (fruits, vegetables, and seeds) are dependent on animal pollination (Klein *et al.* 2007). These authors state that this represents about 35% of human food production. They also evaluated habitat management for pollination for nine crops and found that intensification of agriculture put wild bees and pollination services at risk. However, analyses of FAO data by Aizen *et al.* (2008) show similar trends of increased yields in both pollinator-dependent and nondependent crops. They conclude that this does not support the contention that animal-pollinated crops are currently being affected by pollinator shortages at a global scale. However, they warn that if the disproportionate increase in area cultivated with pollinator-dependent crops continues, dependency on services from dwindling pollinator populations will increase in future.

The value of crop pollination by animals has been calculated in different ways and at different scales with the most recent figures as US \$14.6 billion for the USA (Morse and Calderone 2000) and globally as €153 billion (Gallai *et al.* 2009). Economic valuations are complex and differ greatly between studies, from using values of crops dependent on or benefited directly by animal pollination to including crops indirectly benefiting from animal pollination (e.g., cattle fed on forage crops raised from seed produced by animal pollination).

Introduced European honey bees are our primary crop pollinators. In the USA, numbers of managed honey bee colonies declined from 5.9 million in 1947 to 2.4 million in 2005 (NRC 2007). Invasion and spread of the parasitic mite, *Varroa destructor*, since 1987 has virtually eliminated feral honey bee colonies. The need to control its populations and effects in managed colonies

has increased the costs of beekeeping. Losses of native pollinators due to habitat alteration, pesticides, and other anthropogenic causes are also of concern (Buchmann and Nabhan 1996). Although examples are available from Europe (Biesmeijer *et al.* 2006), there is need for more accurate documentation in North America (NRC 2007).

Effects of land use changes on crop pollination services provided by native bees to alfalfa seed crops in Manitoba, as described by Stephen (1955), may have general applicability. Initial yields are high with low acreage of crop, but yields decrease as the ratio of landscape converted to the crop increases at the expense of habitat for native bees. Several factors change concurrently: loss of nesting and natural foraging habitat for native bees; populations of native bees decrease while numbers of flowers of the crop increase; and distance and area over which bees must forage to service the larger crop acreage increase from suitable habitat remnants.

This chapter presents an overview of biodiversity of bees, those managed for crop pollination, contributions of unmanaged bee populations to crop pollination, and how native bee populations can be enhanced through habitat restoration and management.

1 Biodiversity of bees

Bees are specialized wasps that have changed the diet on which they rear their offspring from animal protein (e.g., caterpillars, spiders) to protein from plants in the form of pollen. Bees exhibit many specialized adaptations for obtaining pollen from flowers and transporting it back to their brood nests (Thorp 1979). Their evolutionary adaptations for obtaining food from flowers and their great diversity make them the most important group of animals that provide pollination services to plants.

The European honey bee (*Apis mellifera*) is what comes to mind for most people when the word “bee” is mentioned, but it is only one of 19,500 species of bee described world-wide (checklist 2008, available at www.itis.gov). This is considerably more diversity than found in all mammals and birds. New species of bee continue to be described. Some estimates would project the global diversity of species to be closer to 30,000 (Michener 2000). If we accept this higher estimate, then bees exhibit more diversity than all mammals, birds, reptiles, and amphibians combined. At more local scales: there are 4,000 species of bee in North America; 1,600 species in California, and over 260 species in Yolo County. The last figure is based on material I have identified for the studies by Claire Kremen on the value of pollination services by native bees to organic and conventional farms (Kremen *et al.* 2002, 2004) and do not encompass all potential bee habitats in the county.

In order to manage and protect bees and the pollination services they provide, it is important to understand the variety of their life histories and foraging behaviors. Bees exhibit several contrasting life-history strategies. Most bees are

solitary, i.e., each female bee constructs her own nest, provisions her brood cells with pollen and nectar, lays an egg on the provisions, seals the brood chamber, and has no further contact with her offspring. Only about 10% of all bees are social in that the life span of the mother overlaps that of her adult progeny and there is some division of labor in the colony. Honey bees and tropical stingless bees have perennial colonies lasting several years. Bumble bees, in contrast, have annual colonies initiated anew each year by mated queens that hibernated over winter. Most of the remaining 15% of bee species are cuckoo bees (cleptoparasites). Female cuckoo bees do not construct nests, but seek out nests of pollen-provisioning bees and lay their eggs in the brood chambers of the host bee. Cuckoo bee larvae usually kill the host eggs or larvae and complete their development on the pollen provisioned by host females.

Most solitary bees are ground nesters. They excavate their burrows in various soil substrates. Some use pre-existing cavities such as beetle tunnels in wood or hollow plant stems; a few excavate their burrows in pithy stems or soft wood. Of these, bees that nest in cavities are the easiest to manipulate and manage for crop pollination. Artificial nest sites can easily be constructed, moved, and stored. The most challenging to manage are bees that nest in soil (Cane 1997).

Most bees are generalists where foraging for nectar is concerned. The important distinctions that relate to pollination services for plant reproduction, efficiency in flower handling for obtaining food resources for reproduction of her young, and evolution of bee–flower relationships, involve differences among behaviors of female bees when foraging for pollen. At the individual level, female bees often exhibit floral constancy, collecting pollen from flowers of the same species throughout one or more foraging bouts. This behavior minimizes handling time. However, at the population level, most bee species are generalist foragers. That is, different females of the same species forage for pollen from different flowering plants. In contrast, females of many bee species specialize on one or a few closely related species of flowering plants as resources for the pollen they need to rear their young. This is termed oligolecty (*oligo* = few, *lecty* = pollen collection).

2 Domestication of crop pollinators

Pollinating insects exhibit many adaptations for obtaining food from flowers. Bees, with their high diversity of species, are considered the most important group of animals that provide pollination services to flowering plants. However, unlike the domesticated plants and animals that have been the focus of this symposium, pollinating insects which service many of our crop plants hardly qualify as domesticated.

Even the European honey bee, which is sometimes referred to as the “domestic” honey bee, differs little from its ancestors. Discoveries by Langstroth (1853) led to the keeping of honey bee colonies in hive boxes with moveable frames. This allowed beekeepers to shift from destroying colonies to remove honey from log or

skep hives to being able to manage and manipulate colonies for honey production. Subsequent selection of honey bee stocks by beekeepers focused on honey production. This primarily involved destruction of queens from unproductive and highly defensive colonies and replacement with queens from more productive and gentler stocks. Mating biology, in which virgin queens fly out of the colony to an area where drones congregate 20 m or more above the ground, mate with several drones in succession, and return to the colony, make it difficult to control breeding. Most managed colonies are open-mated. Beekeepers can exert limited control by flooding an area with drones from colonies of desirable stock or using isolated mating sites. Controlled breeding is possible through instrumental insemination techniques developed less than 100 years ago (Watson 1927). The late Professor Harry H. Laidlaw, Jr., (University of California, Davis) provided a key discovery: the valve fold in the queen's vagina that must be by-passed to allow semen to be efficiently deposited and stored in a virgin queen's reproductive system (Laidlaw 1944). Few beekeepers, or even queen breeders, actually use instrumental insemination. The technique is used primarily by research labs to improve stock, especially with regard to genetic resistance to diseases, for stock maintenance, and for genetic research. Although a few research programs have been directed toward improvement of pollinating activities of honey bees (e.g., Nye and Mackensen 1970, Gordon *et al.* 1995, Page and Fondrk 1995), these stocks have not been adopted by the beekeeping industry. In order for such specific improvements in stocks for pollination to become adopted by beekeepers, pressure and incentives from growers of crops requiring bee pollination will be necessary.

Most other species of bees will mate in confinement where their breeding can be controlled, but little effort has been placed on stock improvement for pollination services or other factors. Breeding in bumble bees, reared in factory-like facilities, focuses primarily on avoiding severe inbreeding problems during production of colonies for pollination. Other managed pollinators tend to be open-mated, as are most commercial honey bees.

3 Managed crop pollinators in North America

Various species of flies are sometimes used by breeders in caged plant populations. However, most managed pollinators for cage, greenhouse, and open field crops are bees. The primary managed crop pollinator is the European honey bee, *Apis mellifera*, which has been distributed virtually throughout the world by humans. Only a few other species of bees are currently managed for crop pollination.

3.1 *Apis mellifera*

The European honey bee is used to pollinate most of the crops that require or benefit from animal pollination. Although not the most efficient pollinator of some crops such as alfalfa (Westerkamp 1991), honey bees can be provided in

sufficient numbers to compensate for low pollination efficiency in many crops (Kremen 2008). Heavy reliance on this single pollinator has raised concerns in recent years. Declines in the numbers of beekeepers and colonies available for crop pollination have been documented (NRC 2007). Various problems in maintaining healthy hives have also arisen, especially due to introduced parasites such as the mite, *Varroa destructor*, and the more recent syndrome, labeled Colony Collapse Disorder (CCD), whose cause is still undetermined. The quest to find the cause of CCD has resulted in major surveys of pathogens (Cox-Foster *et al.* 2007) and pesticides (Mullin *et al.* 2010) in honey bee hives. A single cause for CCD has not been identified. Indeed, it appears most likely that multiple factors work in combination to produce the disorder, as suggested by vanEngelsdorp *et al.* (2009). These concerns have led to considerable new research on honey bee health and have stimulated interest in the potential for non-honey bee species to be managed for crop pollination. During the past 50 years, a few species of non-*Apis* bee have been successfully managed for pollination of crops where honey bees are least effective, such as alfalfa seed, where they quickly learn to steal nectar without tripping flowers, or greenhouse tomatoes, which require vibration (buzz pollination).

3.2 *Megachile rotundata*

The alfalfa leafcutting bee is an accidentally introduced species from the Mediterranean area (Stephen 2003). It is being managed in the western USA to pollinate alfalfa to produce seed of this important introduced forage crop grown throughout much of the world. This bee constructs its leaf-lined brood cells in pre-existing cavities such as wood-boring beetle tunnels. It is managed in domiciles containing human-made tunnels drilled into wood, laminated grooves, or paper or cardboard straws. Throughout most of its range in North America it is multivoltine, with adults active throughout the summer. Sustainable populations of this bee are successfully produced in Canada and sold to seed producers as far south as Imperial County, California.

3.3 *Nomia melanderi*

The alkali bee is native to western North America, but it is also successfully used to pollinate the introduced forage crop alfalfa. It is a gregarious ground-nesting bee. Its specific nest substrate requirements can be duplicated (Stephen 2003) and huge populations of the bee can be managed and maintained (Cane 2008a).

3.4 *Bombus occidentalis* and *B. impatiens*

The western and eastern bumble bees are native to North America, and are used largely by the greenhouse industry to produce tomatoes year-round. Bumble bees are social, but their colonies are annual. Year-round commercial production of

bumble bee colonies became feasible when techniques were developed in the mid 1980s by P.F. Roessler and by R. de Jonghe to circumvent the hibernation period and to make the bees initiate nests under laboratory conditions (Velthuis and van Doorn 2006). The western bumble bee is no longer available in commercial production owing to disease problems in rearing facilities. The common eastern bumble bee is still produced for open field pollination in eastern North America and for use in tomato greenhouses throughout most of North America. At a global scale, the European *Bombus terrestris* is the most widely used managed bumble bee for crop pollination (Velthuis and van Doorn 2006).

3.5 *Osmia lignaria propinqua*

The blue orchard bee (BOB) is a native of western North America. The single generation of adults are active in early spring. It is used primarily for pollination of tree fruits such as apples and cherries (Bosch and Kemp 2001, Torchio 2003). It is a prime candidate for use in almond orchards to supplement dwindling honey bee populations. Since it is a cavity nester, much of the technology developed to manage populations of the alfalfa leafcutting bee is adaptable for management of this species.

Other exotic bees have been introduced and tested, but are not currently being managed extensively for pollination of crops in North America. These include: *Osmia cornifrons*, the Japanese horn-faced bee, which has been occasionally used in apple orchards in the eastern USA (Batra 2003, Stephen 2003); *Osmia cornuta* (Torchio *et al.* 1987) for almond in California, *Pithitis smaragdula* (Daly *et al.* 1971) for alfalfa in California, and *Anthophora pilipes villulosa* (Batra 2003) for blueberry.

Other potential native bees as crop pollinators in North America include: *Habropoda laboriosa* and *Osmia ribifloris* for blueberry (Sampson and Cane 2000); *Osmia aglaia* for raspberries and blackberries (Cane 2008b). Previous authors have provided lists of bees that may have potential as managed crop pollinators (Parker *et al.* 1987) including soil-nesting bees that occur in large aggregations (Cane 1997).

Benefits to diversification of our managed crop pollinators include increasing pollination efficiency, taking advantage of complementary foraging behaviors, providing redundancy, and reducing dependency on a single pollinator species. Local native bees would be the most readily available candidates. If no suitable species are found, introductions of exotic managed species should be considered. Careful consideration of potential environmental risks should be given before any introductions are attempted (Bohart 1962, Thorp 2003). Environmental risks include introductions of contaminant organisms, bees that damage plants, and bees that may displace native species (Bohart 1962). In addition, Thorp (2003) lists genetic alteration of closely related native species and potential enhancement of weed reproduction.

Desirable characteristics of exotic bees to be imported for crop pollination were proposed by Donovan (1990). If importation is deemed valuable, the candidate

species should: be effective pollinators of the target crop; come from an area of similar climate; be free from disease or other natural enemies; be manageable for crop pollination; have a high rate of population increase; and be compatible with native bees and introduced managed honey bees when they overlap in food resource use.

4 Nonmanaged crop pollinators

One of the first surveys of diversity and pollination efficiency of nonmanaged crop pollinators in California was conducted in seed alfalfa by E.G. Linsley (1946). He found many native bee species to be much more efficient pollinators than the widespread, introduced honey bee.

More recent research by Claire Kremen and colleagues in Yolo County, California demonstrated that full pollination of watermelon can be provided by nonmanaged native pollinators on organic farms near wildlands (Kremen *et al.* 2002, 2004). Organic and conventional farms not near wildlands must rely in part or fully on rented colonies of honey bees to obtain full fruit set.

Keys to a successful sustainable system include proximity of farms to natural habitat that supports a variety of bees and the flight ranges of these bees. All pollen-collecting species of bees are central place foragers. Once a nest is established, foraging range is then determined by the flight capabilities of the female bees. A direct relationship has been shown between body size and flight distance (Gathman and Tscharntke 2002, Greenleaf *et al.* 2007).

Similar experiments on watermelon were conducted in New Jersey and Pennsylvania with quite different results (Winfree *et al.* 2007). No detectable effect of native vegetation was found. In these east coast studies, the organic and conventional farms differed primarily in pesticide usage, otherwise all were small-scale farms with multiple crops and no differences in weedy plant abundance or diversity. In this mosaic landscape, all farms were less than 350 m from native vegetation, which is well within the foraging range of most bees. In California, the isolated farms had greater distances to patches of native vegetation. Conventional farms in California were large-scale monocultures with very low weedy flower diversity and abundance, and pesticide use.

5 Habitat management for pollinators

Following studies demonstrating the contribution of nonmanaged pollinators to crop production, the next logical step is to determine whether restoration can effectively and economically enhance pollinator populations on farms. This is most important for organic and commercial farms far from wildlands. These lack sufficient native bee populations to provide full pollination services (Kremen *et al.* 2002, 2004). Projects toward this goal are being conducted in Yolo County, California by Claire Kremen in collaboration with the Xerces Society for Invertebrate Conservation, Audubon California Landowner Stewardship Program,

with citizen scientist monitoring contributions, and cooperation of a number of local growers (Kremen *et al.* 2011). Useful background information on conservation and restorations for pollinators has been published by the Xerces Society (Shepherd *et al.* 2003, Vaughan *et al.* 2007).

Such restoration efforts should enhance populations of native bees and pollination services for small farms not in close proximity to wildlands. However, can sufficient and sustainable populations of unmanaged pollinators be produced to provide significant pollination services for large-scale intensively managed commercial farms? Such farms often have a number of features not amenable to sustainability of pollinator populations in addition to lack of proximity to wildlands with source populations of pollinators, including use of: pesticides harmful to pollinators, herbicides to keep borders weed-free, and crops with short intensive bloom periods.

Set-asides of nonproductive land, such as land in the Conservation Reserve Program (CRP), can be actively managed to provide habitat for foraging and nesting of unmanaged bee populations. How much land is needed? Based on studies conducted in canola in Canada, Morandin and Winston (2006) calculated that 30% uncultivated land within 750 m of the crop would maximize yield and profit. This estimate is in need of testing for different crops and agricultural landscapes.

Other habitats that can be managed to enhance pollinator populations include: urban gardens (Frankie *et al.* 2005, Matteson *et al.* 2008), roadside plantings (Hopwood 2008), powerline easements (Russell *et al.* 2005), greenbelts, golf courses, and green roofs. These all merit further exploration as potential habitat for pollinators.

6 Discussion and conclusions

The search for additional species of bees that can be managed for crop pollination or whose populations can be enhanced and maintained in the vicinity of crops requiring pollination services from bees has received increased attention in recent years. This has been stimulated by increasing stresses on health of honey bee colonies and of the beekeeping industry which have been our primary source of crop pollination services. While we may not be able to domesticate honey bees or other species of bees, many have the capacity to be managed directly or to be enhanced through habitat management for sustainable pollination services. Biodiversity and redundancy of pollinators need to be maintained for the valuable ecosystem service they provide. Conservation of feral bee populations is important for maintaining genetic diversity for future selections of managed pollinators.

Populations of managed pollinators and of unmanaged pollinators, in areas where habitat is being managed, need to be increased each year for sustainability. Populations of native bees in the feral environment may fluctuate considerably from year to year, so their availability in numbers is not consistently reliable. Another major problem is that many crops have large acreages of massive flowering that persists for only a short duration. Thus, there are too many flowers

for too few bees in unmanaged pollinator populations to provide adequate pollination services (Torchio 1990). Provision of stable nest site habitat and of floral resources, especially when nearby crops are not flowering, should reduce some of this fluctuation. Management practices that promote diversity of species should also buffer the system and provide more stability of pollination services (Kremen 2008).

Scale is important for both pollinators and biological control agents. Smaller bees with lower dispersal abilities and smaller foraging ranges require smaller habitats that may be found nesting in and adjacent to crops. Larger bees with large foraging ranges may exist in areas away from crops they visit. Which are more likely to colonize restored habitat on farms? This depends on proximity to suitable source habitats, availability of suitable nest sites, and the poorly understood dispersal abilities of founder females.

The use of multiple species in the same crop needs to be evaluated. Current usage of the alfalfa leafcutting bee in combination with honey bees for alfalfa seed production in California is becoming common (Mueller 2008). Honey bees are not the most effective pollinators of alfalfa (Westerkamp 1991), but given the long growing season of the crop in southern California they can produce an adequate yield. Combined use provides both insurance and efficiency in pollination of the crop. Such systems may integrate the beneficial attributes of multiple pollinators providing redundancy and food-web networks similar to those found in most natural systems. Interactions that could be labeled interference competition may actually be beneficial in enhancing efficiency of pollinators through increasing pollen flow in some systems such as hybrid seed production in sunflower (Greenleaf and Kremen 2006). Research is needed to balance the facilitation of multiple pollinators on crop yield versus the sustainability of pollinator populations that may be competing for the same resources necessary for their own population maintenance and increase.

7

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26 Aquaculture, the Next Wave of Domestication

Dennis Hedgecock

Aquaculture, the fastest growing sector of global food production, accounts for nearly 40% of aquatic production and will soon surpass capture fisheries, forecast to collapse by mid-century. While “animals are not essential” (Harlan, 1995), fish and shellfish make up a substantial portion of human diet, supplying protein and nutrients essential for human development and health. Aquaculture relies largely on natural reproduction or hatchery propagation of wild stocks and boasts few domesticated species (common carp, rainbow trout, Atlantic salmon). There are enormous challenges in conserving while utilizing the planet’s imperiled aquatic biodiversity. Overfishing, introduction of nonnative species, adverse interaction of wild and farmed stocks, and ocean warming and acidification are risks to aquatic genetic resources. The high fecundity of marine fish and shellfish, in particular, creates the risk that release or escape of large, hatchery-propagated families will dilute the genetic diversity of wild populations. Research on developing and improving domesticated stocks for aquaculture should have high priority alongside research on reducing or eliminating interactions with wild populations. There is an opportunity that Jack Harlan would have relished, to document the domestication process in aquaculture, though its course in the human-dominated world is likely to differ markedly from that of plant and animal domestication.

1 Aquaculture

How inappropriate to call this planet Earth, when clearly it is Ocean. (Arthur C. Clarke)

Both Harlan Symposia have naturally focused on the terrestrial species, whose domestication irrevocably changed the course of human history and evolution. Humans have domesticated a remarkably small number of plants and animals for food and fiber, many more plants than animals, although corn, wheat, and rice provide half of the protein consumed by humans. A similarly narrow diversity of animals is the basis of livestock production, and Diamond (1997) has argued that,

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owing to the complex suite of characteristics required, all animals capable of domestication have been domesticated. Certainly, no terrestrial animal is likely to replace the cow, pig, sheep, or chicken. Yet it would be wrong to conclude that domestication is now a matter of history, for a new wave of plant and animal cultivation and domestication is building on planet Ocean.

Globally, per capita annual consumption of fish is 16.4 kg, about 7.8% of total protein consumption, although this ranges by region or country from less than 1 kg to more than 100 kg per person (FAO 2007). While “animals are not essential; plants supply over 90% of the food consumed by humans” (Harlan 1995:240), humans do obtain, in addition to protein, many beneficial nutrients, such as omega-3 fatty acids, from aquatic plants and animals. Until very recently, much of the supply of aquatic living resources came from capture fisheries, which a century ago seemed limitless. Thomas Huxley, the pre-eminent Victorian naturalist, famously stated (Huxley 1883): “I believe, then, that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea fisheries are inexhaustible; that is to say, that nothing we do seriously affects the number of the fish. And any attempt to regulate these fisheries seems consequently, from the nature of the case, to be useless.”

Of course, fishing methods became much more efficient than Huxley could have anticipated, under a variety of technological advances (the steam and diesel engines, radar, sonar, and global positioning systems) and government subsidies that permitted humans to exploit fully and beyond sustainable limits a third of world fisheries by the year 2000 (FAO 2007). According to statistics of the Food and Agriculture Organization (FAO), production from capture fisheries reached a plateau of just over 90 million metric tons (mmt) per year in the 1980s, a figure close to Ryther’s (1969) prediction of 100 mmt based on calculations of global marine primary productivity. The apparent stability in global average production from capture fisheries belies alarming signals of over-exploitation, fisheries collapses, and increasing exploitation of species at lower trophic levels. Indeed, Worm *et al.* (2006) predict the demise of global capture fisheries by 2050. Although debate continues about the status of fisheries, the causes of fisheries collapses, and the path to sustainability (Pauly *et al.* 1998, Myers and Worm 2003, Worm *et al.* 2006, Sibert *et al.* 2006, 2007, Hilborn 2007), capture fisheries, even if managed for sustainable harvests, clearly cannot meet the demand of the 9 billion humans projected for the mid-twenty-first century.

World fisheries supplies have steadily increased – to 155 mmt in 2006, the latest year for which data are available – despite the plateau in capture fisheries production, because of a rapid increase, since the early 1970s, of aquaculture, the farming of aquatic plants and animals (Figure 26.1). Aquaculture now supplies over 40% of all fisheries products and, growing at about 9% per year, will surpass capture fisheries as the dominant source of aquatic food within a few years. The inherent efficiency of producing protein from endothermic organisms in a three-dimensional aquatic environment, compared with traditional livestock species, was pointed out long ago by Bardach *et al.* (1972). Aquaculture can also provide protein with less

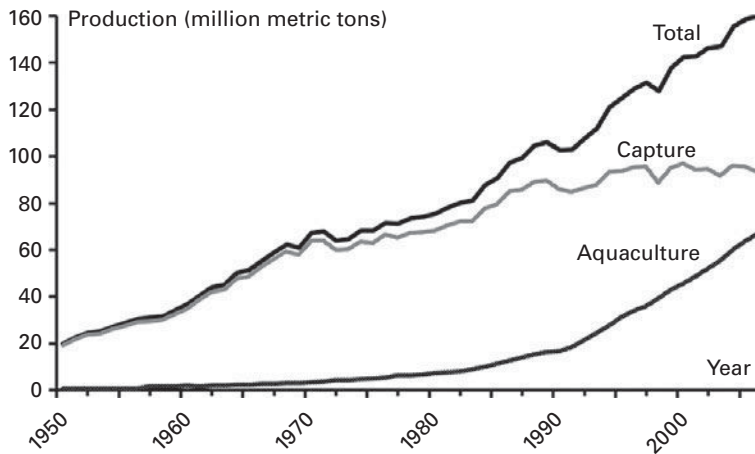


Figure 26.1. World production from capture fisheries and aquaculture (data from FAO 2007). Increases in world supplies since the 1980s have all come from aquaculture.

emission of greenhouse gases and less use of water resources than terrestrial systems; the Los Angeles Times reports, for example, that a six-ounce portion of beef results in the emission of 7,166 CO₂ equivalents, whereas the same amount of steamed mussels produces only 65 CO₂ equivalents (Wiess 2008). Although the negative environmental impacts of salmon and shrimp aquaculture have received attention (e.g., Naylor *et al.* 2000), environmental concerns are being addressed through the development of new technologies, alternative feeds, better management practices, standards for sustainability, and third-party verification. Aquaculture can be done with no more and possibly much less environmental impact than traditional agriculture or poorly managed capture fisheries. Carp aquaculture in central and eastern Europe has been sustainable for about eight centuries; indeed, Balon (2004) provides a remarkable example of sustainability. “Rožemberg pond, which was built in the 16th century and covers 711 ha... still operates on the 2 to 3 year cycle of common carp production (Kourzil & Guziur 2004).” Farming the sea and the domestication of new species for aquaculture are inevitable (Marra 2005).

Aquaculture is generally classified as extensive or intensive, according to the extent of control over environmental factors and input of feed. Extensive aquaculture of herbivorous or omnivorous fish and filter-feeding shellfish accounts for more than 80% of global aquaculture production (Figure 26.2). Stock enhancement, the practice of rearing early life stages in a hatchery and then releasing them into the wild to enhance capture fisheries, might also be viewed as an extensive, albeit inefficient, form of aquaculture.

The phylogenetic diversity of cultivated aquatic species is much broader than that in terrestrial agriculture, comprising fish, sea urchins, mollusks, crustaceans, and red, brown, and green algae (Figure 26.3). Given the diversity of species and culture methods world-wide (reviewed elsewhere: Bardach *et al.* 1972,

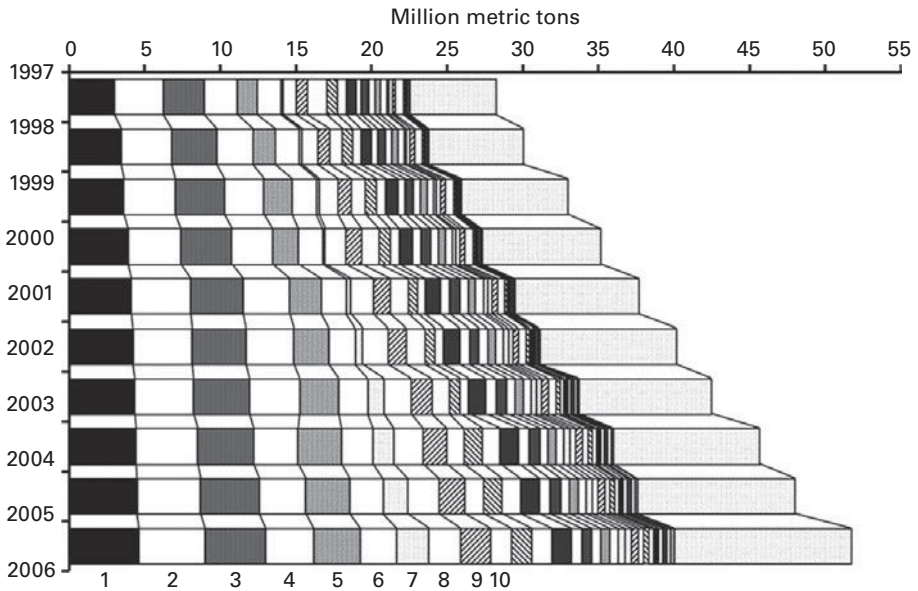


Figure 26.2. Aquaculture production, by species (data from FAO 2007). The upper ranks are dominated by filter-feeding molluscs or herbivorous or omnivorous fishes; production of carnivorous species, which has received much criticism, comprises a small fraction of total aquaculture production. The top ten species are: (1) Pacific oyster, (2) Silver carp, (3) Grass carp, (4) Common carp, (5) Manila clam, (6) Bighead carp, (7) Whiteleg shrimp, (8) Crucian carp, (9) Tilapia, (10) Japanese scallop.

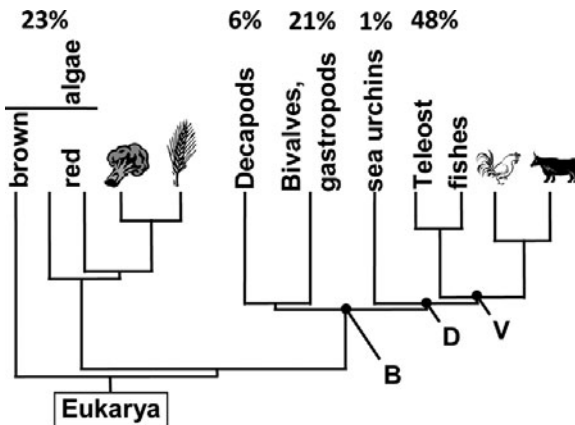


Figure 26.3. Phyletic diversity of aquacultural vs. agricultural species. Percentages above aquacultural species are contributions to global production. Nodes showing the separation of the bilaterian, deuterostome, and vertebrate animal clades are marked B, D, and V, respectively.

Stickney 1986, FAO 2007), a complete review of domestication and conservation of biodiversity in aquaculture is beyond the scope of this short chapter. Rather, the purpose of this chapter is to delineate main issues, primary challenges, and opportunities in aquaculture domestication and conservation of aquatic biodiversity, illustrating these, by necessity, with examples from the limited perspective of personal experience.

2 Domestication of aquatic species

If one takes domestication to mean profoundly changed from wild progenitors, less than a handful of aquatic species have been domesticated: goldfish, common carp, and perhaps two aquarium fishes, guppies and neon tetras (Balon 1995, 2004). These few aquatic domestications, moreover, are quite recent. While fish and shellfish culture trace back to Roman times (e.g., Günther 1897), Balon (2004) dates the domestication of the common carp, in Europe, and the goldfish, in China, both to the twelfth century. Other food species, such as rainbow trout, Atlantic salmon, Pacific salmon, tilapia, channel catfish, and several Asian carp species, as well as aquarium species, such as swordtails, platies, zebra fish, and discus, are regarded by Balon (2004) as in transition to domesticated status. Recently, Duarte *et al.* (2007) called attention to rapid domestication of aquatic species, but their liberal definition of domestication – “breeding, care, and feeding of organisms are controlled by humans” – leaves species unchanged from their wild progenitors, a key criterion in most definitions of domestication. For the most part, aquaculture is in the proto-domestication phase (Harris and Hilman 1989), in which the fish and shellfish are no more than exploited captives (Clutton-Brock 1981). The trend documented by Duarte *et al.* (2007) simply reflects the growth of aquaculture globally. The history of aquatic domestication will be written, perhaps, after another century.

Genetic improvements of domesticated species are well known and widely appreciated. Physiological and morphological changes in aquatic species will likely be just as profound and perhaps more dramatic for their rapidity, since the principles of breeding are now well developed, widespread, and aided by modern molecular and genomic approaches. More importantly, substantial levels of genetic diversity still exist in extant natural populations, from which most aquaculture species continue to be derived. Improvements in yield of c.10%–15% per generation have been obtained in Atlantic salmon, rainbow trout, tilapia, and the Pacific oyster (Bentsen *et al.* 1998, Gjedrem 2000, Langdon *et al.* 2003). The controversy over interaction of farmed and wild Atlantic salmon (see below) testifies to the extent of genetic change in that species and makes a case for considering Atlantic salmon an emerging domesticated species. Insofar as domestication and genetic improvement of aquatic species will increase the efficiency and sustainability of aquaculture, research towards these ends must be encouraged.



Figure 26.4. Growth heterosis (hybrid vigor), evident in the contrast of inbred and hybrid Pacific oysters produced by a factorial cross of two partially inbred lines, suggests that aquaculture yields could be improved several-fold.

Most of the initial improvement in production characteristics of aquatic species, such as the Atlantic salmon, has been based on additive genetic variance and realized by standard methods of individual or family selection. Nonadditive variance is relatively more important in breeding of common carp, perhaps because additive genetic variance has already been fixed during the longer history of carp domestication (Wohlfarth 1993). Nonadditive variance may also be relatively more important in marine species than fresh water species. The Pacific oyster, for example, shows hybrid vigor (heterosis) for yield (Figure 26.4) that is as dramatic as that in maize (Shull 1908, Crow 1998), particularly since it emerges, not from crosses among major landraces, but from crosses among partly inbred lines derived from a single wild population (Hedgcock and Davis 2007). Dramatic heterosis for yield in oysters is associated with equally dramatic levels of inbreeding depression (Evans *et al.* 2004) and mutational load (Bierne *et al.* 1998, Launey and Hedgcock 2001), which is consistent with the dominance explanation of heterosis (Crow 1998) and was predicted by G. C. Williams' (1975) Elm-Oyster model for the advantages of sexual reproduction in species with high fecundity and high early mortality. Since high fecundity and high early mortality are the dominant life history among marine fish (Winemiller and Rose 1992) and invertebrates (Thorson 1950), we might expect considerable scope for genetic improvement and domestication to come from crossbreeding.

3

Conservation

Conservation of genetic resources for agriculture employs strategies and approaches that are often distinct from those employed in conservation of natural biodiversity (seed banks versus protected reserves, for example). Conservation of genetic

resources for aquaculture, on the other hand, is tantamount to conserving natural aquatic biodiversity, since aquaculture is largely exploiting captives from the wild. Thus, the strategies and approaches employed to conserve wild and cultured aquatic species may be similar. The challenges in conserving, while utilizing, the planet's imperiled aquatic biodiversity are enormous and global in nature (Dulvy *et al.* 2003, Jackson 2008). It might be argued that the biodiversity of planet Ocean is more at risk in a human-dominated world with a global economy than was the terrestrial biodiversity of planet Earth at the time of crop and livestock domestication.

The global problem of overfishing has already been mentioned. Jackson *et al.* (2001) argue that overfishing preceded a host of contemporary problems causing disturbance and extinctions in coastal ecosystems. Now, "Synergistic effects of habitat destruction, overfishing, introduced species, warming, acidification, toxins, and massive runoff of nutrients are transforming once complex ecosystems like coral reefs and kelp forests into monotonous level bottoms, transforming clear and productive coastal seas into anoxic dead zones, and transforming complex food webs topped by big animals into simplified, microbially dominated ecosystems with boom and bust cycles of toxic dinoflagellate blooms, jellyfish, and disease" (Jackson 2008).

Coastal ecosystems are characterized as heavily invaded by nonindigenous species (Grosholz 2002); most biological invasions are attributable to shipping via the transport and exchange of ballast water (Ruiz *et al.* 2000), although purposeful, accidental, or inadvertent introductions of nonnative species, owing to aquaculture or the aquarium trade, for example, have also caused profound changes in coastal ecosystems. Purposeful introductions can be curtailed, in principle, with regulations and enforcement, but often these are lacking or insufficient to prevent some intentional or accidental introductions (NRC 2004).

A suite of life-history traits that characterizes the majority of marine fish and shellfish – relatively late maturation, high fecundity, small eggs, long-lasting and widely dispersing plankton-feeding larvae, and broad geographic ranges (Thorson 1950, Winemiller and Rose 1992, Palumbi and Hedgecock 2005) – makes these marine populations more vulnerable to loss of variation and extinction than one might suspect, based on their sheer abundance. These life-history traits appear to be adaptations to a biphasic life cycle, in which larvae disperse to planktonic habitats, far from potentially cannibalistic adults, but face tremendously high, though variable, early mortality. Conservation of such species depends, therefore, not only on protection of adult forms but also on the preservation of a vast, poorly delimited and understood planktonic environment. Conservation of planktonic larval forms has no counterpart in terrestrial conservation.

High fecundity, on the order of a million or more eggs per female per spawning event, and early mortality, typically in the range of 10%–20% per day, makes possible a high variance among spawning individuals in reproductive success, which is defined as the number of offspring contributed to the next generation.

Successful reproduction for most marine animals requires a complex chain of events, from the reproductive maturation and spawning of adults to external fertilization of gametes, development, growth and survival of the larval forms, metamorphosis and recruitment into the adult habitat, and survival and growth of juveniles to maturity. Reproductive activity, though often tuned to the annual seasonal cycle, must still match highly variable local conditions for this chain of events to be complete. The chances of successful reproduction can thus vary dramatically for individuals, perhaps even among individuals adjacent to one another in space but spawning at slightly different times. Consequently, reproductive success in marine organisms might, at times, resemble a sweepstakes lottery, in which there are a few big winners and many losers (Hedgcock 1994).

The hypothesis of Sweepstakes Reproductive Success, which makes testable predictions about temporal genetic change in populations and variance in the genetic composition of new recruits, has received a measure of support from both empirical (e.g., Li and Hedgcock 1998, Hauser *et al.* 2002, Turner *et al.* 2002, Hedgcock *et al.* 2007, Lee and Boulding 2007) and theoretical studies (Waples 2002, Hedrick 2005, Eldon and Wakeley 2006). The implication of this hypothesis for conservation is that these seemingly inexhaustible living marine resources may have effective population sizes that are orders of magnitude smaller than census sizes and, thus, rates of genetic drift and inbreeding that may erode biodiversity on ecological time scales.

Adverse interactions of wild and hatchery-propagated stocks are likely growing with the global expansion of aquaculture (McGinnity *et al.* 2003, Hindar *et al.* 2006) and stock enhancement programs (Born *et al.* 2004). High fecundity creates the risk that release or escape of large, hatchery-propagated families will dilute the genetic diversity of wild populations. Ryman and Laikre (1991) first called attention to this problem, using a simple mixing equation to determine the effective size of a fish population comprising both naturally (wild) and artificially (hatchery or captive) propagated components, $\frac{1}{N_e} = \frac{x^2}{N_c} + \frac{(1-x)^2}{N_w}$, where N_e is the effective population size of the mixed population, N_c is the effective size of the captive or hatchery population, N_w is the effective size of the wild component, and x is the proportion of the spawning population of hatchery origin. In the marine realm, where fecundities are higher than for fresh water species, the risk that an enhancement program might dilute genetic diversity of a wild population is great but manageable with appropriate data and care (Hedgcock and Coykendall 2007).

One way to eliminate much of the risk of interaction between wild and hatchery stocks is to render farmed stocks sterile. Triploidy can be induced in bivalve mollusks and even some fish; triploid animals tend to be effectively sterile and can be cultured in the wild with little risk that they will spawn and release planktonic and highly dispersing offspring into the coastal environment. The ability to culture triploids thus frees aquaculture to pursue the benefits of domestication while minimizing or preventing the interactions of farmed and wild stocks.

4 Conclusions

Research on developing and improving domesticated stocks for aquaculture, together with research on reducing or eliminating interactions between wild and farmed populations (e.g., by inducing triploidy in hatchery-propagated stocks) should have high priority.

There is an opportunity that Jack Harlan would have relished, to document the domestication process in aquaculture, though its course in the human-dominated world is likely to differ markedly from that of plant and animal domestication.

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27 Genetic Sustainability and Biodiversity: Challenges to the California Dairy Industry

Juan F. Medrano

Issues and challenges related to the California dairy industry are examined in this chapter. This industry is a prime example of a very productive animal production system that has rapidly evolved in the Central Valley of California. The Central Valley, with its favorable climate, expanse of land for crop production, and proximity to agricultural byproducts that are fed to cattle, has favored the enormous success of this industry. However, there are many challenges facing California dairy productivity that will need to be addressed in the near future. The focus of this discussion will be on issues related to production efficiency, biodiversity, and breeding in the dairy animal population.

1 Overview of the California dairy industry

California has been the USA's leading dairy state since 1993 (CDFA 2007a). As shown in [Figure 27.1](#), from 1950 to 2007 milk production has increased 580%, topping 40 billion pounds of milk in 2007, which constitutes 24% of the USA dairy supply. The number of animals has increased 130% to 1.8 million milking cows, while the number of dairies has gone down 80%, resulting in large production units averaging 600 cows, with some in excess of 3,000 cows (CDFA 2007a). The productivity of this industry exemplifies a large-scale animal production system (CAST 1999) that has taken advantage of scale economies to reduce cost of production, processing, and marketing, and over the past few decades, the industry has enjoyed very good economic times. The large production of milk has positioned California as a primary exporter of dairy products. Dairy products rank as the third largest agricultural export of the State of California with a value of US\$604 million in 2006 (CDFA 2007b). Butter, nonfat powder, and cheese account for 77% of the milk product (Dairy Marketing Branch 2007), playing a major role in how the industry transforms the abundant supply of milk into exportable commodities. The production of cheese has propelled the growth of the industry, increasing 648% in the past 23 years from 305 million pounds in

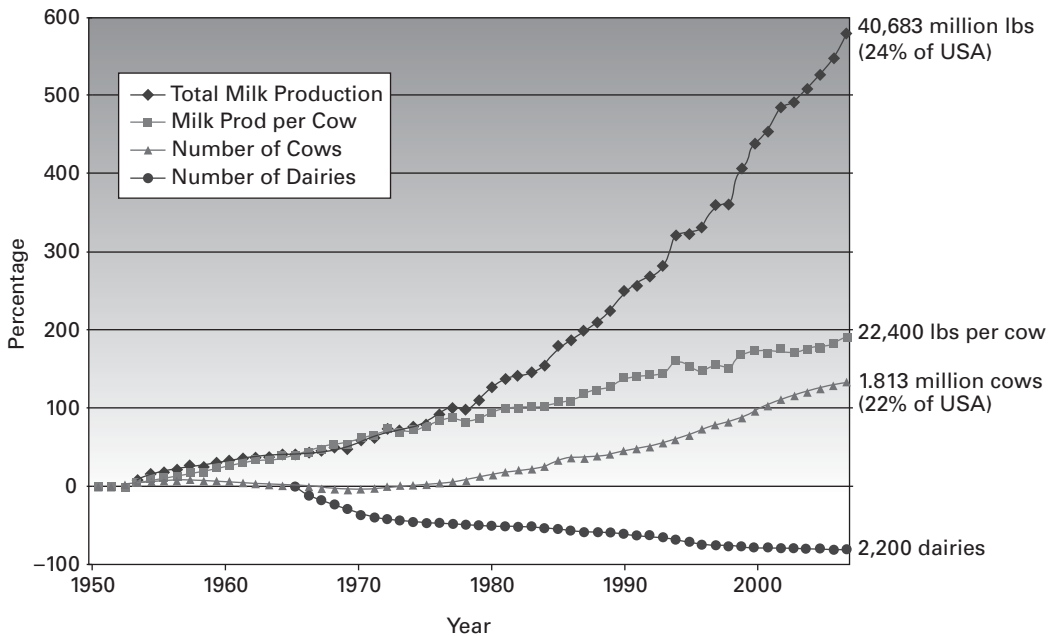


Figure 27.1. Comparative changes in the California dairy industry from 1950 to 2007: total milk production (5,991 to 40,683 million lbs or 2.7 to 18.5 million metric tons), production per cow per lactation (7,710 to 22,400 lbs or 3,497 to 10,165 kg), number of cows (777 to 1.813 million cows), number of dairies from 1965 to 2007 (11,300 to 2,200 dairies) (USDA-NASS).

1984 to 2.3 billion pounds, accounting for 47% of the milk in 2007 (Dairy Marketing Branch 2007).

Recently, the industry benefited from periods of very high milk prices, in the range of US\$20 per hundredweight in 2007 (Dairy Marketing Branch 2007). But as the prices of milk soared, the costs of feed and fuel also went up throughout the state (Robinson 2008). Cost of feed has been impacted by increased demand and also by a reduction of cultivable acres of land due to urbanization. Some of the shortfall in feeds, like alfalfa, were supported by imports from surrounding states. The price of corn, an important feedstuff of the industry, skyrocketed in 2007–8, partly because of the increased use of corn for ethanol production in the Midwest. Following the economic downturn, milk prices went down 32% in 2009 from the average prices paid to producers in 2008. These fluctuations in milk prices and feed costs are major economic challenges for the industry that will likely force changes in feeding practices, emphasizing the use of locally produced forages for rations to reduce the cost of imported commodities (Robinson 2008). These constraints will also require further increases in animal productivity by culling low-producing cows and increasing the production efficiency of the dairy population.

2 Animal diversity

There may truly be said to be a constant struggle going on between, on the one hand, the tendency to reversion to a less perfect state, as well as an innate tendency to new variation, and, on the other hand, the power of steady selection. . .¹

Dairy production in California is a large-scale animal production system. These large-scale systems typically utilize large numbers of animals and an intensive feed-input system with efficient management control over production and processing to increase productivity and reduce waste (CAST 1999). In California, the dairy intensification process has been driven by rising demand and markets for dairy products and has been facilitated by the introduction of new technologies, including significant advances in biotechnologies. The development of large-scale animal production systems has spread beyond North America and Europe to many parts of the developing world because of output demands and reductions in available land for pastoral systems (FAO 2007). Therefore, examining the issues and challenges of dairying in California is of value in relation to global sustainability of milk as an essential nutrient of the world food supply.

One common feature of large-scale animal production systems is that they are based on a few breeds (FAO 2007). In this respect, dairy cattle represent the extreme case, where one major international breed, Holstein, predominates world-wide. The prominence of Holsteins is no surprise, since early in the history of the breed, superior milk production records were documented. By 1923 the Holstein–Friesian Association was the largest of all the cattle breed associations, recording 1.3 million animals in its Herd Book (Sanders 1925). The breed composition in the United States dairy-cow gene pool, including purebred and cross-breeds for cows born in 2005 was 90.8% Holstein, 6.3% Jersey, 0.9% Brown Swiss, and 2% other minor breeds (Powell *et al.* 2008). Hence, Holstein cows are the cornerstone of the genetic pool given the task to sustain the milk consumption demands in the USA and world-wide.

The North American Holstein gene pool is dominated by a few elite sires that are disseminated world-wide by breeding companies through the use of artificial insemination. About 80% of the cows are bred by artificial insemination and about 25,000 calves are born from elite females using embryo transfer. A good example of the reproductive potential of elite Holstein sires comes from the bull named Elevation, born in 1965. He had over 80,000 daughters, 2.3 million granddaughters, and 6.5 million great-granddaughters (VanRaden 2007). Elevation had a significant impact on the Holstein breed and by 2005 his relationship or impact on the breed was 15.2% (Hansen 2006).

One direct consequence of intense genetic selection in Holstein, leading to rapid genetic improvement together with the global dissemination of germplasm, has been the reduction of genetic diversity of the population. Intense selection leads to rapid genetic improvement but also reduces the relative number of effective parents of each sex in the population, or the effective population size (N_e). In

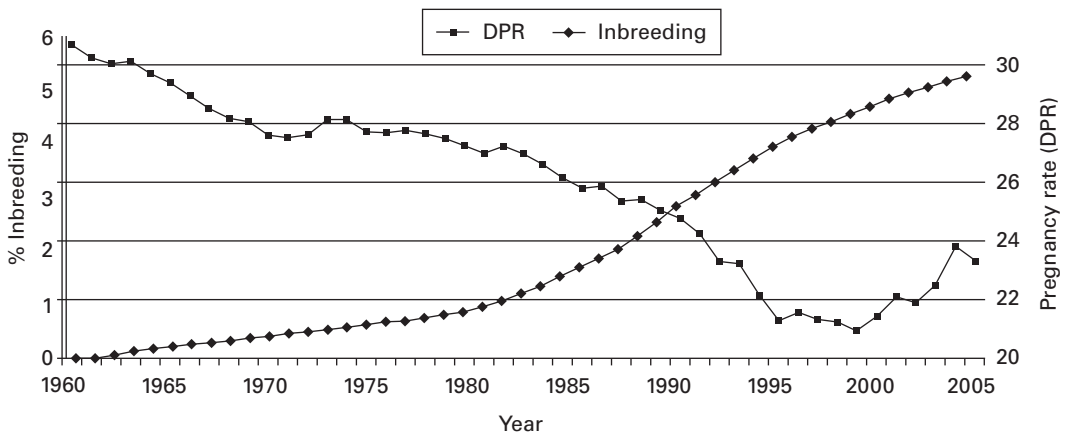


Figure 27.2. Change in the level of inbreeding and daughter pregnancy rate (DPR) in US Holsteins from 1960 to 2006. DPR measured how quickly cows become pregnant again after having a calf. Data from USDA-AIPL.

Holsteins worldwide, estimates of effective population size range from 100 to 150, which has resulted in approximately 5% inbreeding (Young and Seykora 1996, Hayes *et al.* 2003, VanRaden *et al.* 2004), in spite of the fact that there are more than 3.7 million Holstein cows enrolled in milk recording in the USA (Hansen 2006). Inbreeding of Holstein females in the USA from 1994 to 2004 has increased at a constant rate of 0.1% per year (Figure 27.2). This level of inbreeding is not unique to Holsteins. Jerseys, the second most abundant dairy breed in the USA, had a 7.0% inbreeding in 2005 and rate of increase of 0.20% inbreeding per year from 1994 to 2004 (Hansen 2006).

Inbreeding results in reduction in mean phenotypic performance in inbred animals, or what is referred to as inbreeding depression (Falconer and Mackay 1996), and can have a considerable economic impact on dairy productivity. Inbreeding can negatively affect traits like milk production, fertility, and survival (Mc Parland *et al.* 2007). Breeders make consistent efforts to control levels of inbreeding in their animals by examining pedigree relationships and preventing the mating of closely related individuals. However, until now, it was not possible to know exactly how inbred an individual offspring will be from a given mating or what the ancestral effect on genetic diversity of the population has been. The inbreeding coefficient is calculated as a probability that an individual receives identical-by-descent alleles from its ancestors (Falconer and Mackay 1996). However, new technologies using genotypic data can estimate the fraction of total DNA that two individuals share, allowing for more accurate predictions of relationship and inbreeding (VanRaden 2007) and, in turn, supporting a more sustainable breeding and management of reproductive traits.

One of the primary concerns of the effects of inbreeding is on reproduction and fertility. Trends for reproductive traits in the US dairy herds show that all

indicator traits related to reproduction have had a decline in recent years. For example, daughter pregnancy rate (DPR), a measure of how quickly cows become pregnant again after having a calf, has declined in Holsteins from 33% to 23%, from 1960 to 2007 (Figure 27.2). Similarly, services per lactation, the number of inseminations necessary for a cow to become pregnant, has increased from 2.1 services in 1996 to 2.6 in 2005 (Norman *et al.* 2008).

Concerns about inbreeding and reduction of animal diversity with the associated negative consequences on fertility, health, and survival have engendered an increasing interest in utilizing crossbreeding in dairy cattle. However, of the cows born in the USA in 2005 only about 1.6% were crossbreds (Powell *et al.* 2008). Crossbreeding has been applied largely by breeding Holsteins horizontally with another high-producing dairy breed, rather than introducing an exotic low-producing breed (Maki-Tanila 2008).

3 Animal breeding overview

Man can do only a few kinds of things to change the heredity of his animals. First of all he has some power to decide which of them shall have many offspring, which shall have few and which shall have none. That is selection. Selection can be based on individuality, on ancestry, on progeny, or on combinations of these.²

This section provides a brief overview of current methods utilized in dairy cattle breeding as background for discussing new developments applying genomic technologies that have significantly transformed current breeding practices. Breeding utilizes genetic variation with the aim of procreating animals for a given production and economic environment, which implies the development of breeding goals. Breeding generally occurs at two levels: one that produces genetic improvement, which involves a relatively small number of elite animals in the population, and one that disseminates the genetic material and produces the final farm product. As an economic and biological activity, breeding requires the development of goals and the definition of traits and phenotypes of economic value, and the emphasis that should be placed on each trait in a given environment.

Genetic progress in dairy cattle depends mainly on the merit of sires, so young sire candidates are evaluated based on pedigree, progeny, and sib tests, or a combination of these, in order to reliably rank the animals. The data are analyzed to select breeding animals expected to have the highest performing offspring for a combination of traits. The USDA has produced genetic evaluations for dairy traits since 1935. The list of traits evaluated has escalated to include, in recent years, traits related to health, fertility, and longevity. Table 27.1 shows ten dairy traits that are currently included in the national economic selection indexes with the year they were introduced and the current emphasis placed on each trait (VanRaden 2007).

In large-scale dairy breeding, great emphasis is placed on the accuracy of prediction of an animal's breeding value, or the value of an animal judged by

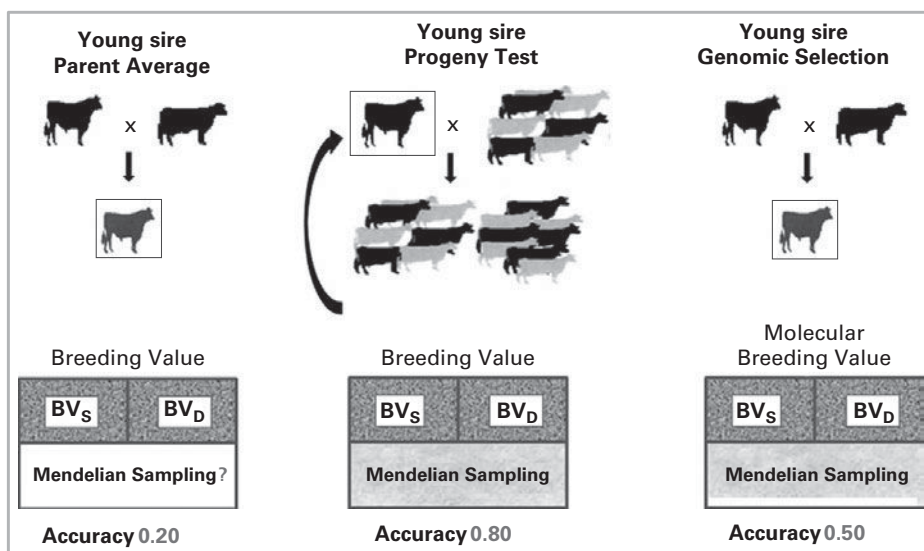


Figure 27.3. Diagram of designs utilized in the estimation of breeding value of dairy sires from parental information, progeny testing, and genome-wide selection. The boxes below represent the sources of information utilized in the estimation. A_S is the sire breeding value, A_D is the dam breeding value. Mendelian sampling represents the unknown Mendelian random segregation of the alleles an individual receives from his parents. The accuracy of the estimation of breeding value improves considerably from parent average estimation by progeny testing a sire with 100–200 daughters where the effect contributed by Mendelian inheritance is estimated by the performance of the daughters. The estimation of molecular breeding values based on prior knowledge of SNP effects significantly improves accuracy from parent average estimation.

the mean value of its progeny (Falconer and Mackay 1996). Sires are ranked to select the best parents based on breeding value. The breeding value of young sires is initially estimated from their pedigree by averaging the breeding value of their sire and dam. This initial evaluation has very low reliability (approximately 20%) because of the uncertainty of the assortment of genes that are received from each parent by random Mendelian segregation. In order to develop reliable estimates of breeding value, preselected young sires are progeny tested by mating them to a random sample of cows in the population and estimating their breeding value from the performance of their daughters (Figure 27.3). This is a lengthy and costly process that takes five years or more in order to produce 50–100 daughter records to reach an approximate 80% reliability for the prediction of breeding value, and the cost is in the range of US\$50,000 per bull (Powell *et al.* 2003, Schaeffer 2006). However, this approach has been extremely effective and has resulted in the 2% genetic gain per year in the US Holstein population, worth US\$5 million per year (VanRaden 2004). An important contribution to this success has been the periodic revision of selection goals and traits (Table 27.1), and the utilization of national selection economic indices introduced by USDA in 1971 (VanRaden 2004).

Table 27.1. Emphasis placed in dairy traits in national genetic–economic selection indices and year the trait began to be included in the indices

Genetic-economic selection indices combine genetic parameters and economic values into a single measurement that is calculated for each animal and used for selection. Currently 54% of the emphasis is placed in improving functional traits, which exclude the first two categories of Milk, butterfat and Protein.

Trait	Year begun	Emphasis (%)
Milk, butterfat	1935	23
Protein	1977	23
Calving ease	1978	2
Udder support	1983	6
Feet and legs	1983	3
Size	1983	−4
Longevity	1994	17
Mastitis resistance	1994	9
Fertility	2003	9
Stillbirth	2006	4

Source: Table from VanRaden 2007.

Central to animal breeding is the estimation of the response to selection or genetic gain per unit of time ($\Delta G/t$),³ which is directly proportional to accuracy of selection, selection intensity, genetic variation, and generation interval (Falconer and Mackay 1996). Using these factors, the genetic gain from selection can be predicted. This prediction is an important tool to define optimum selection schemes and directions of change in a population. Selection intensity reflects the proportion of animals that are used as parents for the next generation. In dairy cattle, the widespread use of artificial insemination has resulted in a significant reduction in the number of sires. Accuracy depends on the quantity and quality of performance records available. Based on these records the breeding values of individuals are predicted and the animals with the highest merit are selected as parents. It is important to maintain genetic variance to obtain a continuous genetic response. Generation interval is the amount of time required to replace one generation and it determines the progress per unit of time. This is important from the standpoint of genetic progress and one of the drawbacks of progeny testing dairy bulls, in that it takes a long time to get an accurate estimate of breeding value. The longer interval between generations that results from use of progeny test in selection tends to offset the advantage of an accurate selection (Dickerson 1944). Therefore, new technologies that can improve the accuracy of selection and reduce generation interval will have a significant impact on development of more flexible selection goals to meet the challenges of the dairy industry.

Selection tends to reduce the genetic variance of the population related to an increase in inbreeding. In selected populations, superior families contribute more offspring to the next generation than average families, resulting in increases in the rate of inbreeding compared to an unselected population (Bijma *et al.* 2000).

In dairy cattle, breeding, maintaining the genetic variance, and avoiding inbreeding for the long term are important parameters. Statistical methods have been developed that allow optimizing the long-term response and restricting rates of inbreeding (Meuwissen 1997, Bijma *et al.* 2001, Rutten *et al.* 2002) and have resulted in more sustainable breeding programs. In addition, there is interest in expanding crossbreeding in dairy cattle (Hansen 2006).

4 New technologies: genomic selection in dairy breeding

Suppose that we were given a reasonably complete map of all of the chromosomes, showing the location of all important genes affecting the character in question as well as of convenient marker genes. What could we do with it?⁴

We are now beginning to answer the above question, posed by Sewall Wright in 1939. With the development of the Bovine Genome Project, investigators now have the tools to identify the gene contributions to traits of economic importance in cattle and to integrate this knowledge into breeding programs (Figure 27.4). Recently, the draft bovine genome sequence was utilized to identify a large number of single nucleotide polymorphisms (SNPs) (Van Tassell *et al.* 2008) to develop tools to interrogate the genetic variation in cattle. SNPs are DNA sequence variations that occur when a single nucleotide (A, T, C, or G) in the genome sequence is altered. Because SNPs occur frequently throughout the genome and tend to be relatively stable genetically, they serve as excellent genetic markers. These markers can be used for gene mapping, genomic selection, inbreeding and pedigree analysis, and traceability.

A first-generation bovine SNP high-density genotyping array has been developed consisting of 54,000 SNPs (BovineSNP50) uniformly distributed across the whole bovine genome with an average SNP spacing of 51.5 kb. The SNP chip was validated in beef and dairy cattle breeds and it is a robust tool to perform whole genome-association studies and for applications of whole genome selection. In whole genome-association studies, a dense set of SNPs is usually genotyped in a large group of individuals in a population to identify regions of the genome that can be associated with measured phenotypes (Hirschhorn and Daly 2005). This approach has been used in humans to survey variation associated with disease and to identify quantitative trait loci associated with health traits. In contrast, the application of this technology in livestock provides the means for direct application of genomic technologies to animal breeding programs.

As mentioned above, in the traditional dairy animal breeding model, selection of sires is based on estimating their breeding value based on progeny testing. The model assumes that a large number of genes with small effects as well as nongenetic causes determine the phenotype. In this model, the genotype of an individual at specific loci is unknown and selection is based on the predicted effect of the genes an individual carries or its predicted breeding value. In 2001, Meuwissen (Meuwissen *et al.* 2001) proposed an alternate approach to estimate breeding values, referred to as whole

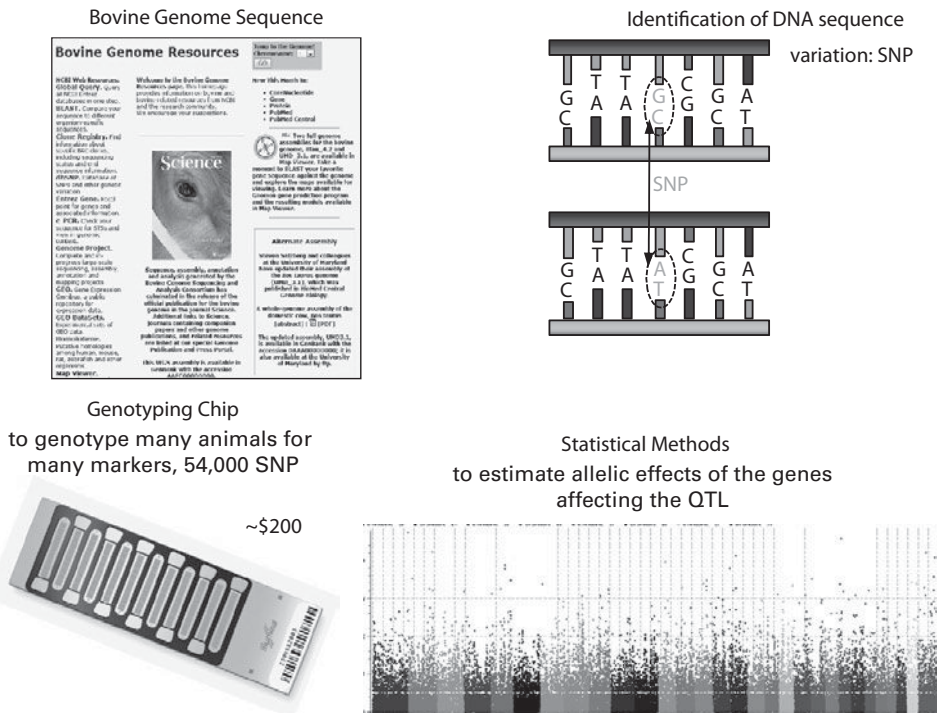


Figure 27.4. Diagram of new enabling genomic resources and technologies that are available to query the bovine genome in pursuit of applied strategies of whole genome selection. The bovine sequence and a large number of genomic resources can be accessed through databases at The National Center for Biotechnology Information (<http://www.ncbi.nlm.nih.gov/genome/guide/cow/>) (NCBI 2008). The large-scale identification of single nucleotide polymorphisms (SNP) or DNA sequence variation is central to querying marker associations in the genome. Bovine genotyping SNP chips are commercially available through Illumina (<http://www.illumina.com/applications/agriculture/livestock.ilmn>). Statistical methods for SNP analysis are central to the application of whole genome selection.

genome selection (WGS), that uses a dense set of genetic markers covering the whole genome so that the genetic effects of the QTL could be explained by the markers (Goddard 2009). WGS encompasses the idea of predicting the total genetic value of an animal by estimating its breeding value, using information on variation in DNA markers (Goddard and Hayes 2007) (Figure 27.3).

It is expected that the application of WGS will impact the cost efficiency of dairy breeding programs by shortening the generation interval and improving the accuracy of selection of young sires and reducing the need for progeny testing all sires. WGS has been applied for the evaluation of dairy sires combined with traditional evaluations. To develop the system in the United States, 5,335 Holstein bulls were genotyped for 38,416 markers using the Bovine SNP50 chip. A training data set of 3,570 bulls born before 1999 were used to predict current breeding value estimates for 1,759 bulls born from 1999 to 2002 for 21 traits. The reliability of

breeding value predictions from genomic information was 50% for young bulls, compared with 27% for the traditional parent average (VanRaden *et al.* 2009). This represents a very significant average increase of 23%. These results have enhanced the information available to breeders, revolutionizing the industry's approach to breeding to the extent that genomic prediction has become a standard in the industry, complementing the traditional breeding value estimations. An added benefit of genomic prediction is the relatively low cost of genotyping with the BovineSNP50 chip: in the range of US\$200 per animal.

Application of genomic selection will benefit the dairy industry and will contribute to the sustainability of dairy breeding by:

- (1) Increasing the accuracy of breeding value prediction with minimal cost to inbreeding;
- (2) Decreasing generation interval;
- (3) Providing the ability to overcome age and sex limitations for milk production traits;
- (4) Providing a direct link between the genetic evaluation and the genome;
- (5) Contributing to selection for new traits that are difficult to measure, such as milk composition traits and feed efficiency; and
- (6) Developing knowledge about the physiological process on which selection acts.

5 Sustainable animal breeding

A vision of sustainable farm animal breeding and reproduction has been put forward by the European FABRE Technology Platform (<http://www.fabretp.org/content/view/21/43/>), suggesting opportunities for improving the biological and economic efficiency of food production systems linking the environment, the consumer, and the economy. As shown in Figure 27.5, animal breeding and reproduction are at the top of the animal production pyramid, defining the quality of the animals used in agriculture. The criteria for sustainability define areas of emphasis in response to societal concerns to produce safe and healthy food and high-quality products, while maintaining the health, genetic diversity, and efficiency of domestic animals with concern for the environment. Opportunities exist to improve the sustainability of the breeding and reproduction systems in dairy farming by using technologies targeting declines in reproduction and increases in incidence of diseases such as mastitis, digestive problems, and lameness, while maintaining high levels of productivity. Central to addressing these issues is the improvement of the estimation of breeding values by the application of multi-trait genetic-economic selection indices (Table 27.1) by utilizing whole-genome selection tools, and the expansion of crossbreeding programs to maintain genetic diversity of the animals.

New genomic tools provide the opportunity to fine tune genetic selection schemes between organisms and environments, animal welfare and health, genetic

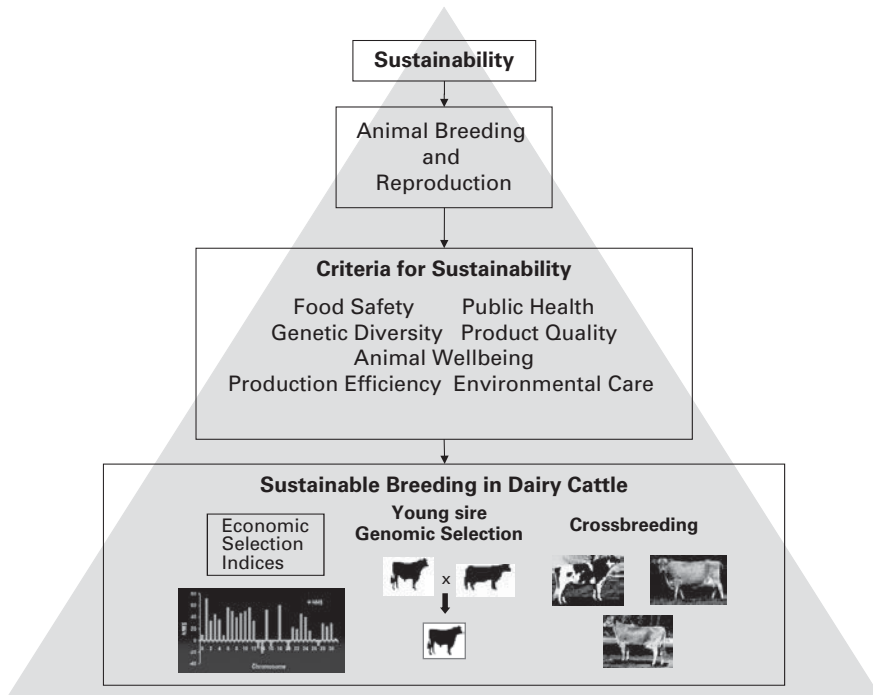


Figure 27.5. Animal breeding and reproduction are at the top of the animal production pyramid, defining the quality of the animals used in agriculture. The criteria for sustainability defines areas of emphasis in response to societal concerns and stewardship of our animals. Sustainable breeding in dairy will be realized by the application of genetic–economic selection indices, the application of genomic tools to contribute to the estimation of breeding values, and by the expansion of crossbreeding programs to maintain the genetic diversity of dairy animals. (Diagram modified from EFFAP <http://www.effab.org/Breedingis.aspx>.)

diversity and product safety. Therefore, the challenge, and our focus in coming years, will be the integration of new technologies to support the genetic sustainability and biodiversity for the California dairy industry.

Notes

- 1 Caption to the chapter on Conservation of Genetic Variance in Michael Lerner’s classical book *The Genetic Basis of Selection* (Lerner 1958). Lerner was for 25 years a poultry geneticist at UC Berkeley who made significant contributions to population and evolutionary genetics and animal breeding.
- 2 Quote from Jay L. Lush’s book *Animal Breeding Plans* (Lush 1945). Lush is considered the father of modern animal breeding. He was a pioneer animal geneticist who showed how genetics and mathematics can help in solving problems of animal breeding.
- 3 $\Delta G/t = \frac{(r_{A,\hat{A}})(i_p)(\sigma_A)}{L}$ where genetic gain per unit of time $\Delta G/t$, is proportional to the accuracy of selection or the correlation between breeding values and their prediction $(r_{A,\hat{A}})$, the

intensity of selection (i_p), the standard deviation of breeding values or the square root of the additive variance (σ_A) and the generation interval or the time that it takes to replace one generation (L).

- 4 Early visionary quote (Wright 1939) by Sewall Wright (1889–1988), a mammalian geneticist considered one of the founders of theoretical population and evolutionary genetics.

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